THE CRANIAL MUSCULATURE AND TAXONOMY OF CHARACOID FISHES OF THE TRIBES CYNODONTINI AND CHARACINI

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CONTENTS

SYNOPSIS

The cranial and some other musculature of characoid fishes of the tribes Cynodontini and Characini is described and compared. The tribes are redefined on the basis of myological and associated osteological characters. It is shown that some of these characters are shared specializations which unite the tribes in the subfamily Characinae.

An attempt is also made at a functional description of the jaw mechanism of *Rhaphiodon*.

A remarkable example of parallelism is noted between a cynodontid (*Rhaphiodon*) and a cyprinid fish (*Macrochirichthys*). The cranial musculature of the latter is described.

INTRODUCTION

THROUGHOUT the extensive literature on the Characoidei (see, for example, the bibliography in Gery, 1972b) few references have been made to the myology of these fishes. Those that do make only brief comment on particular features. Of earlier works, that of Grenholm (1923) describes the pectoral girdle muscles of *Salminus* and *Alestes*, Holmquist (1911) the hyoid muscles of *Hydrocynus*, and Nelson (1949) the pectoral muscles of *Rhaphiodon*.

Of more recent work, that of Kampf (1961) deals with the cranial muscles of *Hydrocynus* and presents a functional analysis of the jaw mechanism. Robert's (1969) work on some predatory characoids, although an osteological study, makes reference to some cranial muscles. Winterbottom (1974) has figured and referred to the branchial arch muscles of *Brycon*.

The most comprehensive account to date of comparative myology in the characoids has been that of Alexander (1964). In that work the author describes the cranial muscles of some diverse neotropical genera. Later, Alexander (1965) again commented on the cranial musculature of some characoids when comparing them with siluroids.

This present study is part of a wider ranging one, planned to cover the cranial myology of all major characoid families. A preliminary survey suggested that a more limited study of some 'specialized' predatory taxa might be fruitful in establishing the primitive or advanced nature of certain characters in the skeleto-muscular systems of these fishes and thus provide pointers to phyletic relationships.

Two groups of species are considered in this paper, the Cynodontini and the Characini. These are treated as tribes and the subfamily which they constitute (the Characinae) is restricted to those taxa sharing certain myological and osteological specializations not found in members of the Characinae *sensu* Weitzman (1962) (referred to in this paper as the Tetragonopterinae ; see p. 239). The subfamily name is restricted because of the inclusion of the type genus *Charax* in the tribe Characini (see Myers, 1949).

A remarkable example of parallelism is noted between the characoid *Rhaphiodon* and the cyprinoid *Macrochirichthys*. A description of the cranial musculature of the latter is included as an Appendix to this paper.

METHODS AND MATERIALS

Specimens were dissected on their right side (both sides in some cases). The drawings were made using a Wild M4 and M5 drawing apparatus. Details were added freehand using high power magnification. The drawings were reversed to facilitate comparison with those of other authors.

As well as the material listed below, specimens representing species of all characoid families were dissected.

List of specimens used (all radiographed) :

Species	BMNH register number	Standard length (mm)
Acanthocharax microlepis	1971.10.17:1444–1460	47, 63; alizarin preparation, 62
Asiphonichthys stenopterus	1944.2.29:2	42
Charax gibbosus	1972.7.27:832–846	103–70 (including alizarin preparation, 95)
Charax gibbosus	1878.1.21:6	skeleton
Cynodon gibbus	1972.7.27:43–45	196, 198 ; dry skull
Cynopotamus argenteus	1895.5.17:237	147

Cynopotamus argenteus	1872.6.18:24	skeleton
Cynopotamus goeldii	1912.10.31:20	116
Cynopotamus lineasquamis	1897.11.26:4	150
Cynopotamus magdalenae	1972.7.27:847–854	100, 100, 105; alizarin preparation, 80
Exodon paradoxus	Unregistered	55
Genycharax tarpon	1895.11.16:100	78
Gnathocharax steindachneri	1935.1.25:2–4	22
Heterocharax macrolepis	1926.10.27:97–110	43–46
Hydrolycus pectoralis	1927.6.7:4–5	220
Hydrolycus scomberoides	1972.7.27:46–49	190, 197, 203
Hydrolycus scomberoides	1866.8.14:122	skeleton
Hydrolycus scomberoides	Unregistered	dry skull
Macrochirichthys macrochir	1922.5.19:1	400
Macrochirichthys macrochir	1866.5.2:46	216
Macrochirichthys macrochir	1898.11.8:121	skeleton
Opsariichthys uncirostris	1923.3.5:6–12	150
Opsariichthys uncirostris	1901.3.6:9	skeleton
Rhaphiodon vulpinus	1935.6.4:34–39	230; alizarin preparation, 93
Rhaphiodon vulpinus	1893.4.24:30–31	325, 305
Rhaphiodon vulpinus	1897.12.1:184	dry skull
Rhaphiodon vulpinus	1881.7.2:17	600
Roeboides dayi	1920.12.20:25–29	90
Roeboides guatemalensis	1909.3.12:11–15	87
Roeboides myersii	Unregistered	115
Roeboides prognathus	1935.6.4:256–65	alizarin preparation, 110
Roestes alatus	1924.3.3:46–48	84–95

ABBREVIATIONS USED IN TEXT FIGURES

Muscles and connective tissues

A_1, A_2a, A_2b, A_3 A_W Divisions of the *adductor mandibulae*

AAP	*Adductor arcus palatini*
ABP	*Abductor profundus*
ABS	*Abductor superficialis*
AD	Accessory depressor muscle
AO	*Adductor operculi*
ARD	*Arrector dorsalis*
ARV	*Arrector ventralis*
DO	*Dilatator operculi*
EPAX	Epaxial muscles
HH	*Hyohyoideus*
H-HT	*Hyohyoideus*-hypohyal tendon
HY-SHT	*Sternohyoideus*-hypobranchial tendon
HY-UT	Hypobranchial-urohyal-*rectus ventralis* tendon
HYPAX	Hypaxial muscles
IM	*Intermandibularis*
LAP	*Levator arcus palatini*
LAT.S	*Lateralis superficialis*
LO	*Levator operculi*
LS-PT	*Lateralis superficialis*-pterotic tendon
OBV 1–4	*Obliqui ventrales*
PH	*Protractor hyoideus*
PHCE	*Pharyngoclavicularis externus*
PHCI	*Pharyngoclavicularis internus*
RC	*Rectus communis*
RV	*Rectus ventralis*
SBA	Swimbladder appendices
SCA	*Supracarinalis anterior*
SH	*Sternohyoideus*
SHD	Dorsal division of *sternohyoideus*
SPO	*Sphincter oesephagi*
TCT	Tendinous connective tissue
TRV	*Transversus ventralis*
VT	Ventral tendon of *adductor mandibulae*

Skeletal elements

bas	Basihyal	Lpma	Ligament connecting the premaxilla with the maxilla
bp	Basihyal projection (thickened tissue)	Lpp	Ligament connecting the preopercle and pterotic
c1–5	Ceratobranchials	Luh	Ligament connecting the urohyal and hypohyal
ce1–6	Centra	max	Maxilla
ch	Ceratohyal	ns	Neural spines
cl	Cleithrum	op	Operculum
cor	Coracoid	pmx	Premaxilla
df	Dilatator fossa	po	Preoperculum
ep	Epihyal	prb	Pleural ribs
hyo	Hyomandibula	ps	Parasphenoid
hyp	Hypohyal	pte	Pterotic
imb	Intermuscular bones	ptt	Post-temporal
io	Interoperculum	rs	Rhinosphenoid
Laep	Ligament connecting the retroarticular and epihyal	q	Quadrate
Laq	Ligament connecting the anguloarticular and quadrate	sc	Supracleithrum
Lihp	Ligament connecting the interhyal and preopercle	sn	Supraneurals
Lmp	Ligament connecting the maxillary and palatine bones	sp	Sphenotic
		sy	Symplectic
		tr	Tripus
		ur	Urohyal

In all drawings muscles are indicated by thin continuous lines, tendons by thin dashes, ligaments by thick parallel dashes and connective tissue by alternating dots and dashes. Bones are indicated by outline or shaded by stippling.

Tribe **CYNODONTINI** Fowler, 1958

Cynodonidi Fowler, 1958
Cynodontinae Eigenmann, 1909
Sarcodacinae (part) Gregory & Conrad, 1938
Rhaphiodontinae Travassos, 1946
Cynodontidae Greenwood *et al.*, 1966

The species belonging to this tribe are characterized by their compressed, tapering bodies which bear minute scales. The ventral midline of the body is markedly keeled. The mouth is obliquely aligned to the horizontal axis of the body. All the teeth are conical, those at the anterior of the lower jaw being enlarged, sabre-like canines. The teeth are arranged in a single row in both jaws and the maxilla is toothed for its entire length.

The pectoral fins are very long, extending to a point just beyond the centre of the standard length. The dorsal fin is short-based (II 10 rays), the anal long-based (*c.* III 35–80 rays).

The overall coloration of the fishes is silver, some species showing dark humeral and caudal blotches and red pectoral, ventral, adipose and caudal fins.

Species are recorded from the Orinoco and Amazon systems ; from the Essequibo in Guyana ; from Surinam ; and from the La Plata–Paraguay systems (Schultz, 1950 ; Boeseman, 1952). Specimens appear to have been collected from only the larger rivers. Some species grow to large size. Schultz (1950), for example, records a skin of *Rhaphiodon vulpinus* of 690 mm standard length, while a specimen in the British Museum measures 600 mm S.L. Lüling (1972) figured the head of a specimen of *Hydrolycus* sp. estimated to have been at least 1 metre in length.

Eigenmann (1909, 1910) and Regan (1911) both ranked this group of taxa as a subfamily, but neither commented upon its possible relationships with other characoids.

Gregory & Conrad (1938) included the group in their Sarcodacinae on the basis of superficial morphology.

Greenwood *et al.* (1966) recognized the group as a family, but no diagnosis was given.

Gery (1972b) recognized the subfamily Rhaphiodontinae (following Travassos, 1946 ; see below) and noted that it may be related to the Characinae (= Characini in this paper).

The most complete anatomical study made on any cynodontine species was that of Nelson (1949) who studied the internal anatomy of *Rhaphiodon vulpinus*, principally the swimbladder and Weberian apparatus. He also described and figured the skull and pectoral girdle and briefly commented upon the pectoral musculature.

Weitzman (1962) has described part of the Weberian apparatus of *Rhaphiodon* and *Hydrolycus*, and Roberts (1969) has commented upon certain other osteological features of *Rhaphiodon* (see p. 212).

The genera and species have been revised most recently by Schultz (1950) and the nomenclature used in that paper is adopted here.

Some confusion seems to have arisen concerning the correct application of the names *Cynodon* and *Rhaphiodon*. Travassos (1946, 1951–52) has considered the nomenclatural history of these genera and he concluded that *Cynodon* is a *nomen nudum*. Although it is not relevant to debate the nomenclature in a paper of this nature, the name *Cynodon* does appear to be valid (see Whitehead & Myers, 1971 : 496, para. f), and hence the replacement of Cynodontinae by Rhaphiodontinae (Travassos, 1946) is unjustified.

For reasons stated in this paper (p. 226) the genus *Roestes*, previously assigned to the Characinae (*auct.*) is now considered to be a member of the tribe Cynodontini.

Description of the Cranial Musculature

The following myological descriptions are based on specimens of *Cynodon gibbus*, *Rhaphiodon vulpinus*, *Hydrolycus pectoralis* and *H. scomberoides* (Fig. 1A, B & C).

Facial musculature (Figs 2–6)

The *adductor mandibulae* is composed of sections A_1, A_2a, A_2b and A_w. I have considered A_2 to consist of two divisions rather than representing two separate muscles, i.e. A_2 and A_3, because there is a medial exchange of fibres before insertion ; there are no separate tendons of insertion ; and the sites of origin of the muscle are in accordance with it being a single functional unit.

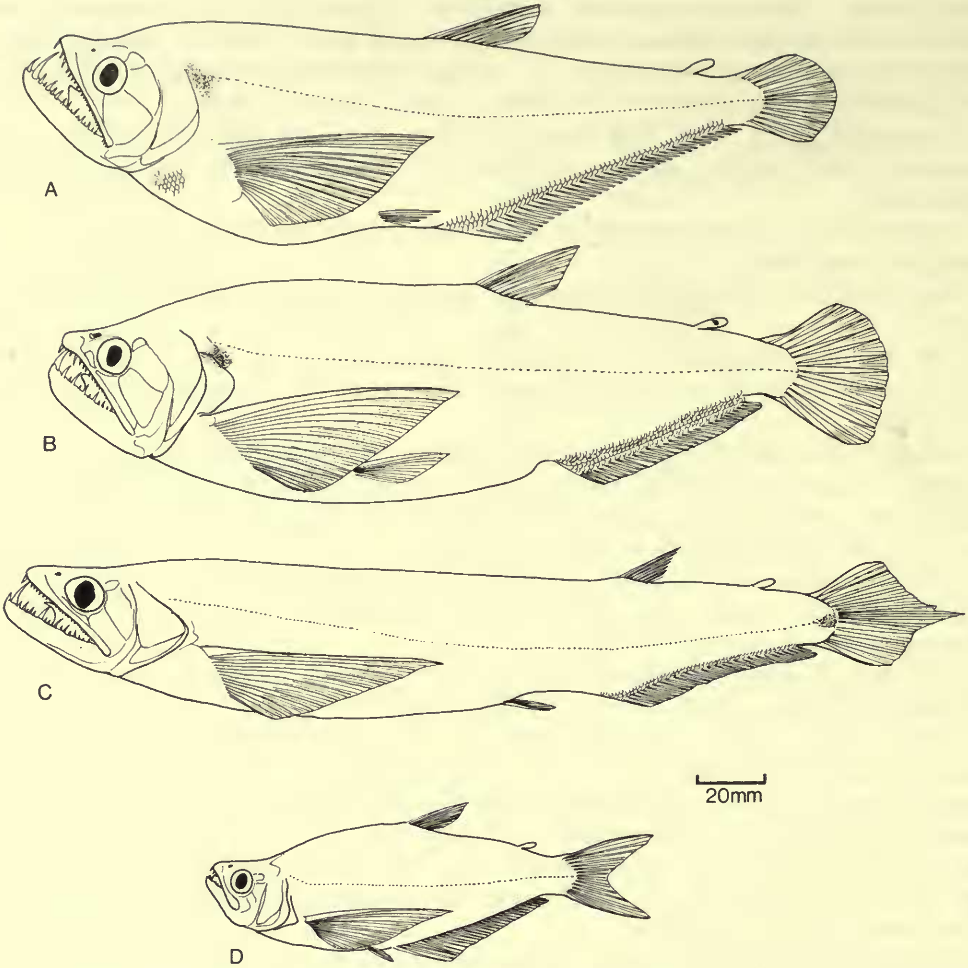

Fig. 1. Outline drawings of (A) *Cynodon gibbus*, (B) *Hydrolycus pectoralis*, (C) *Rhaphiodon vulpinus* and (D) *Roestes alatus*. All drawn to scale.

Alexander (1964) identified the innermost elements of the *adductor mandibulae* in *Hoplias*, *Serrasalmus*, *Myleus* and *Leporinus* as A_3. However, I regard the inner division of the muscle in *Hoplias* as A_2b. A 'precursor' of the condition seen in *Hoplias* is found in *Alestes macrolepidotus* (pers. obs.) where a medial element has become separated from the main body of the muscle but lies against the ventromedial surface of the *levator arcus palatini*, seemingly without finding strong attachment to the hyomandibula. I believe that an element in *Leporinus* can also be identified as A_2b. The situation in *Serrasalmus*, however, is more complex and the muscle may well represent A_3. The only other characoid I have examined in which I can definitely define A_3 is *Bivibranchia*, where the muscle has become completely detached from the body of A_2 and runs from the hyomandibula to insert on the ectopterygoid.

Adductor mandibulae section A_1 (Fig. 2). This is a small triangular slip of muscle originating from the ventral edge of the quadrate. The fibres run dorso-anteriorly at an angle of 40° to insert upon the medial dorsal surface of the angulo-articular. Some fibres are seen to pass anteriorly into the extensive band of connective tissue which covers the medial surface of the maxilla and which posteriorly joins the maxilla to the lower jaw. Unlike the condition encountered in other characoids (Bryconini, Alestinae, Hydrocyoninae) there is no separate maxillary-mandibulary ligament (of Alexander, 1964 (= *ligamentum primordiale* of authors)). The 'ligament' is in fact a thickening of the collagenous fibres along the border of that connective tissue which forms a covering to the floor of the orbital cavity, and which extends along the medial face of the maxilla. This arrangement of the tissue allows very little movement of the maxilla (cf. *Charax*, p. 230).

Anteriorly the maxilla is connected to the premaxilla by a short thick ligament (Lpma, Fig. 2). The premaxilla in turn is firmly united to the median ethmoid by a ligament embedded in a sheet of tissue.

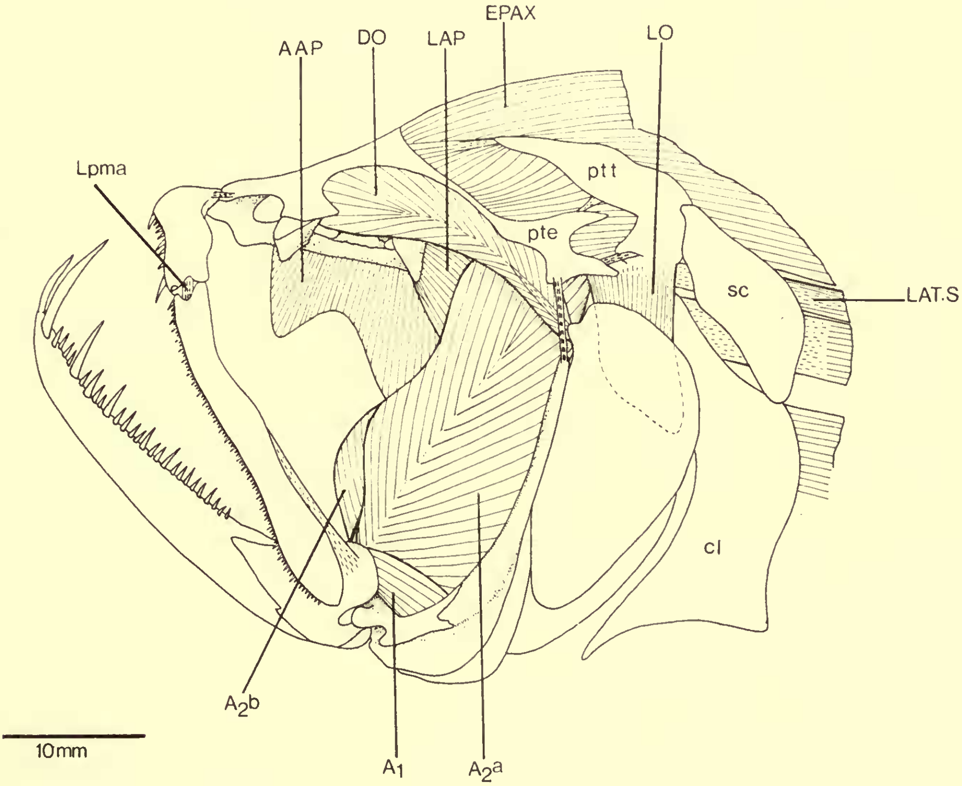

FIG. 2. *Cynodon gibbus*, superficial facial musculature, lateral view. The maxillary has been pulled down to expose the posterior of the lower jaw. The dashed line on the operculum shows the extent of the *levator operculi*.

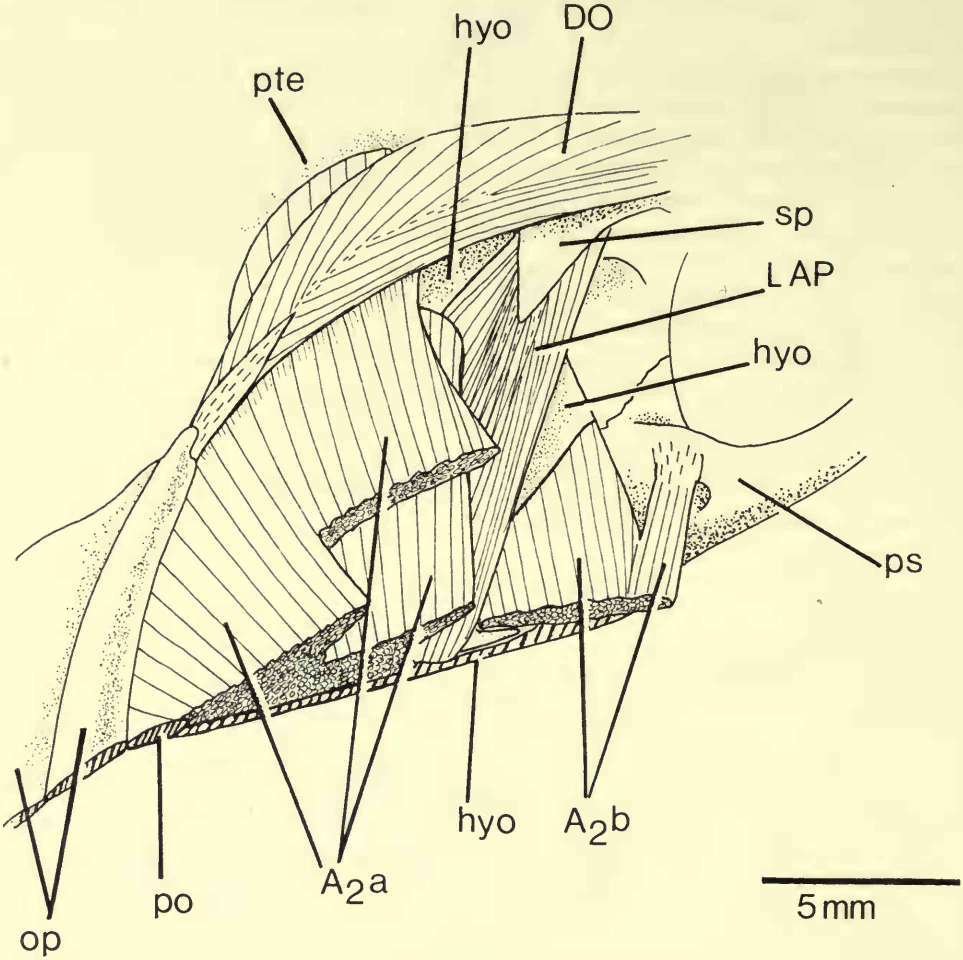

FIG. 3. *Cynodon gibbus*, oblique ventral view of the dorsal section of the *adductor mandibulae* to show its various sites of origin. The muscles and bones have been cut through.

Section A_2 of the *adductor mandibulae* is an extensive and complex element covering the cheek. Dorsally the muscle is divided into outer and inner elements by the *levator arcus palatini*. Between these runs the *ramus mandibularis* V with branches serving both elements.

The outer element (labelled A_2a) takes its posterior origin from the preoperculum, the fibres running ventrally at an angle of 5–40° to insert upon an extensive tendinous sheet which forms the medial face of the muscle. These fibres are met along a medial raphe by those stemming from the pterotic and which run almost perpendicularly (Fig. 3). Medially the muscle has a third point of origin, from the dorso-lateral aspect of the hyomandibula. These fibres also run vertically to insert with those originating from the pterotic. Thus, although at first sight the lateral face of the muscle appears to be formed of two discrete parts, close examination reveals that there is a continual interchange of fibres along the raphe. The orbital face of the muscle is curved in the shape of a shallow S.

Ventrally, a tendon (VT, Fig. 4) runs from the preoperculum, at the point of the quadrato-preopercular suture, to join the aponeurotic system. The more medial ventral fibres of the muscle insert into this tendon. (The tendon is variously developed in the characoids and is most highly so in those long-jawed forms (Hepsetidae, Salminae and Erythrininae) where the *adductor mandibulae* is extensive (pers. obs.)).

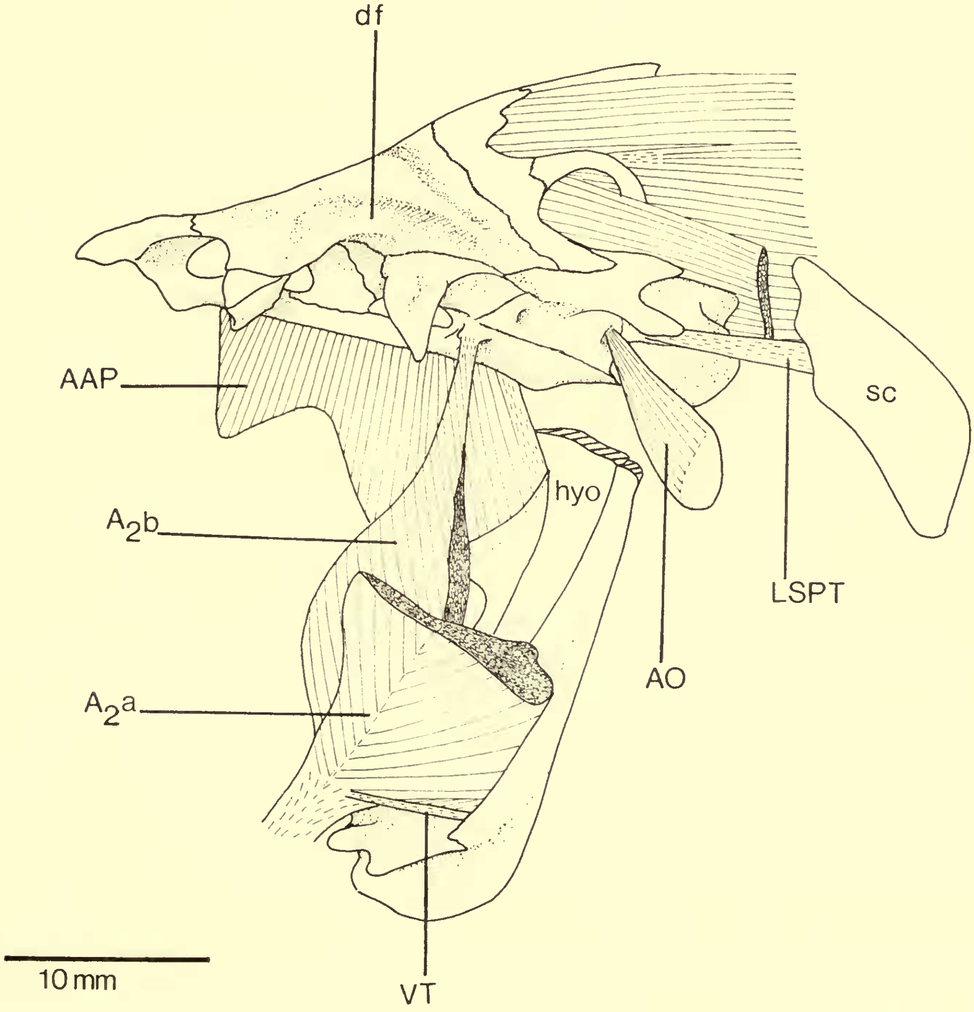

FIG. 4. *Cynodon gibbus*, deeper facial musculature, lateral view. The *adductor mandibulae* has been cut through to show the entire *adductor arcus palatini*. The superficial epaxial musculature has been removed.

The inner element (labelled A_2b) originates posteriorly from the dorso-lateral aspect of the hyomandibula and anteriorly from the lateral wing of the parasphenoid (Figs 3 & 4). The anterior origin is somewhat tendinous and involves only a thin segment of the muscle.

A_2b is separated from A_2a by the interposition of the *levator arcus palatini*. Immediately below this separation, however, the two elements are closely applied. A_2b becomes greatly thickened ventrally and its antero-dorsal margin curved around the orbit to lie in the same plane as A_2a. The epimysial tissue covering the surface of A_2b grades into a thicker (? collagenous) tissue at the leading edge of the muscle ; this wraps around the lower margin of the ectopterygoid and covers the inner face of the suspensorial bones, extending across the metapterygoid-quadrate fenestra. Roberts (1969 : 417) remarks that the metapterygoid-quadrate fenestra is lacking in *Rhaphiodon* but is replaced by a thin translucent sheet of bone. In the specimens I have examined the fenestra has always been present. It may be that in some cases there is an extreme thickening of the 'collagenous' tissue covering this opening.

A_2a and A_2b merge together into the aponeurotic sheet. The aponeurosis is complex ; medially that part of the sheet which derives from A_2b extends as a thick tendon into the lower jaw to lie perpendicularly across the angulo-articular (Fig. 5).

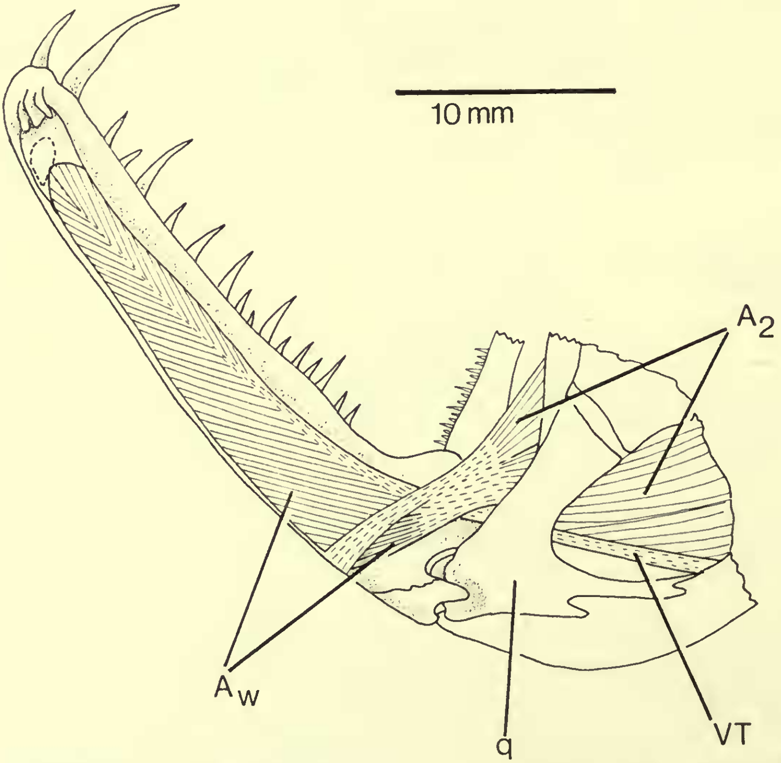

FIG. 5. *Cynodon gibbus*, lower jaw musculature, medial view. The dotted line indicates the position of the *intermandibularis*.

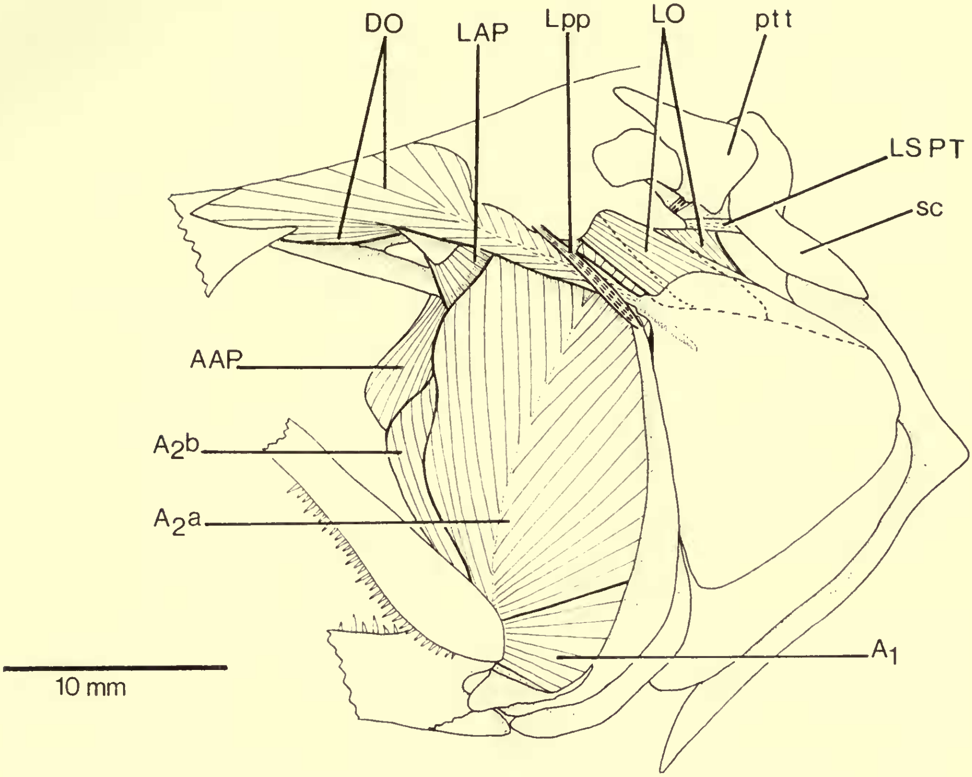

FIG. 6. *Rhaphiodon vulpinus,* superficial facial musculature, lateral view. The long dashed line on the operculum shows the extent of the *levator operculi*; the short dashed line indicates that of the *adductor operculi.*

It provides the posterior border for the fibres of the *adductor mandibulae* section A_w. Lying laterally to this extension, at an angle of 45° and stemming from A_2a, is another tendon, from which arises another series of fibres contributing to A_w; these pass laterally and converge with the main mass of the muscle. The dorsal border of A_w is formed by a long tendon originating from the aponeurotic sheet and running along the ventral border of the thick tooth trench. Anteriorly it descends, dividing the muscle. The fibres vary in alignment to the horizontal body axis from 10° to 30°.

The form of the *adductor mandibulae* is almost identical in *Cynodon* (Fig. 2), *Rhaphiodon* (Fig. 6) and *Hydrolycus.* The same complexity of origins and insertions is apparent.

In all genera the hyomandibular bone is reduced, as compared with that in other characoids. That is to say, instead of the bone being in the form of a compressed plate-like element it is reduced to a slender strut (Fig. 7).

In *Cynodon* the hyomandibula exhibits a lateral flange and it is this border which provides the site of attachment for the *adductor mandibulae* A_2a, A_2b stemming from the medial aspect of the bone (see p. 240). In *Rhaphiodon* and *Hydrolycus* the

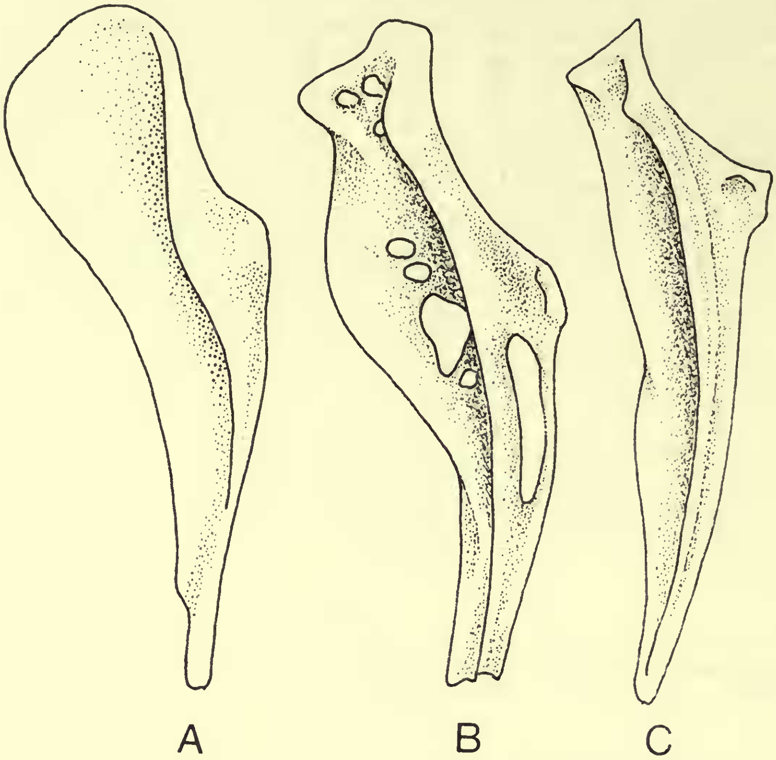

FIG. 7. Hyomandibular bones of (A) *Cynodon gibbus*, (B) *Rhaphiodon vulpinus* and (C) *Hydrolycus scomberoides*. Drawn to same size.

hyomandibula is similarly modified. However, in *Hydrolycus* the lateral flange is curved to face anteriorly, whilst that of *Rhaphiodon* displays a condition somewhat intermediate between those seen in the other two genera (Fig. 7).

Levator arcus palatini (LAP, Figs 2 & 6). This is a large pyriform muscle, the apex of which originates from the sphenotic process. The anterior bundles of fibres originate from long tendons. Insertion is upon the face of the hyomandibula between the two elements of the *adductor mandibulae* A_2. In *Cynodon* some posterior fibres of the *levator* merge with those of both A_2a and A_2b.

The degree of development and orientation of the muscle are about equal in *Cynodon*, *Rhaphiodon* and *Hydrolycus*.

Adductor arcus palatini (AAP, Figs 2, 4 & 6). In *Cynodon* this muscle originates along the length of the parasphenoid (Figs 2 & 4) to insert ventrally upon the dorsolateral aspects of the endopterygoid. Latero-posteriorly the muscle is covered by the *adductor mandibulae* A_2b. Its posterior margin is bordered by a wide tendon and the muscle inserts into a shallow depression on the hyomandibula.

In *Rhaphiodon* and *Hydrolycus* the origin of the muscle is confined to the posterior part of the parasphenoid (Fig. 6). In all genera a thick band of collagenous fibres runs along the medial face of the endo- and ectopterygoid bones. This tissue is an extension of that which covers the base of the parasphenoid and serves to attach the suspensoria to the lateral margins of that bone.

Levator operculi (LO, Figs 2 & 6). This is a compressed trapezoidal element originating anteriorly from the pterotic. Laterally and posteriorly the fibres take their origin from a horizontal tendon (LS-PT, Figs 4 & 6). (This tendon is not to be confused with the ligament which joins the posttemporal with the intercalar and which lies just medial to it (Figs 2 & 6).) This tendon is the termination of the *lateralis superficialis* of the body musculature. It passes across the medial surface of the supracleithrum to which it is attached by connective tissue, to insert finally on the posteriorly directed pterotic process.

In *Rhaphiodon* the exposed opercular section of the tendon is long (Fig. 6). In *Cynodon* and *Hydrolycus* it is short and thick and provides a face of origin for only a few of the muscle fibres, the remainder stemming somewhat tendinously from the outer surface of the post-temporal. Insertion of the muscle is medially along the dorso-posterior surface of the operculum. In *Rhaphiodon* the muscle extends as a crescent some way around the posterior margin of the operculum (Fig. 6).

Adductor operculi (AO, Fig. 4). The origin of this muscle, through a rather thin tendon, is from the subtemporal fossa which lies on the exoccipital just anterior to the lagenar capsule. The fossa is shallow and is barely visible in a large skull of *Rhaphiodon* (90 mm in length).

The muscle takes the form of a rather compressed cone and is directed laterally at an angle of about 10° to the perpendicular. The area and position of insertion vary in different genera. In *Cynodon* it inserts into the centre of the *levator operculi*, whereas in *Hydrolycus* it runs somewhat anteriorly to the *levator*. In *Rhaphiodon* the *adductor* covers a wide area of insertion following that of the *levator*.

Although both the *adductor* and *levator operculi* insert together, the fibres do not become confluent but retain their identity to their points of insertion.

Dilatator operculi (DO, Figs 2 & 6). In all three genera this muscle has two origins. One is dorsally from the frontal-sphenotic groove or fossa which extends on to the cranial roof ; the other is ventrally from the deep cavity which lies between the frontal and the orbitosphenoid.

In *Hydrolycus* some ventral fibres of the muscle also take their origin from the sphenotic process.

The muscle is asymmetrically bipinnate, the tendon of insertion running close to the ventral border. The anterior and ventral fibres are long and are directed into the raphe at a shallow angle. Those stemming from the dorso-posterior borders are short and acutely angled. The tendon is thickened at its insertion upon the anterior dorsal process of the operculum.

In *Rhaphiodon* the insertion is into a bony tube formed along the lateral face of the operculum (Fig. 6).

In *Cynodon* a well-developed frontal ridge forms the anterior and lateral borders of the dilatator fossa. In *Rhaphiodon* the borders are less well defined being formed medially by the edges of the frontal fontanel.

The *dilatator operculi* is most highly developed in *Rhaphiodon* where it covers the entire frontal area (Fig. 6).

In all species the muscle is covered only by the skin of the head.

The preoperculum is connected to the pterotic by a thick ligament (almost ossified in some specimens). The ligament passes over the *dilatator operculi* and obscures its point of insertion on the operculum.

Hyoid musculature (Figs 8–10)

In all genera the hyoid musculature is of almost identical arrangement.

Protractor hyoidei (PH, Fig. 8). This muscle extends from the second, third and fourth branchiostegal rays to cover the ceratohyal and part of the epihyal. The *protractor hyoidei* of each side passes over the first branchiostegal rays to unite with its counterpart into a single unit running anteriorly to insert dorsally and ventrally to the *intermandibularis*.

The medial, unpaired part of this muscle is divided by a λ-shaped myoseptum. The two latero-dorsal bundles insert via fine tendons into the skin covering the floor of the mouth ; the single ventral bundle is flattened towards its insertion which is by means of two thin, laterally placed tendons attaching to the dentaries on either side of the symphysis.

Dorsally, at the point where the two lateral sections of the muscle join into the single, medial element, there arises a large area of connective tissue which extends to cover the basihyal. Anteriorly the tissue becomes thickened, forming a prominent projection (bp, Fig. 8). Widely spaced, possibly elastin, fibres can be detected in this tissue. Below this layer is another which is closely bound to the basihyal and which joins that element to the hypohyals. This deeper layer is much denser, and the fibres running from the face of the hypohyals appear to be somewhat tendinous.

Intermandibularis (IM, Fig. 8). This muscle is thick, and oval in cross-section. The form of this muscle is almost identical in all three genera.

Hyohyoidei (HH, Fig. 8). The elements of this muscle are weakly developed (the term 'weak' is used here to denote the condition as compared with that in most Cyprinoidei and Siluroidei (Takahasi, 1925 ; Matthes, 1963 ; Winterbottom, 1974 ; pers. obs.)). This degree of development is not only characteristic of the Cynodontini but is evident throughout the Characidae, Hemiodontidae, Erythrininae and in the long-jawed predatory groups, Acestrorhynchinae, Ctenoluciidae and Hepsetidae. However, in other characoid families such as the Prochilodontidae, Anostomatidae and Curimatidae, the *hyohyodei* is more complexly arranged and well developed (pers. obs.).

In many teleosts two sections of this muscle are generally recognized (Millard, 1966 ; Osse, 1969 ; Winterbottom, 1974). However, in the Cynodontini (and in some of the other taxa mentioned above) the division appears to be rather arbitrary and one based on topographical, rather than anatomical grounds (although, of course, a functional difference cannot be ruled out).

The origin of each division is from a short tendon attached to the ventral hypohyal of the opposite side, the tendons crossing antero-ventrally to the hypohyals. This entire site is covered with a connective tissue sheet that extends from the basihyal ; it is, in fact, a continuation of the tissue that connects the basihyal and the *protractor hyoidei* (see above, p. 224 and Fig. 8).

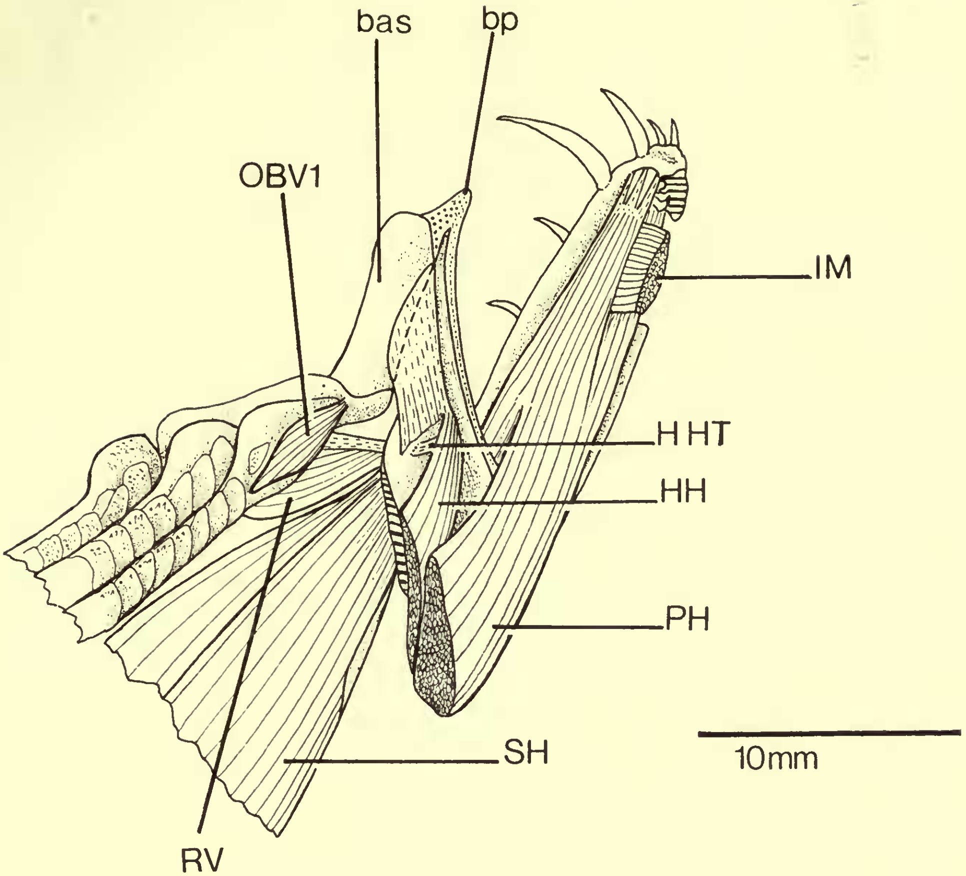

FIG. 8. *Cynodon gibbus*, hyoid musculature, dorso-lateral view. The hypohyal, *protractor hyoideus* and *hyohyoideus* have been cut through. The basihyal is shown entire but the tissue and process anterior to it have been cut along the midline.

The *hyohyoidei* is separated from the *protractor hyoidei* by a thin fascia of tissue as it passes on to the ceratohyal and between the branchiostegal rays. The fibres are closely applied to the branchiostegal membrane, the number of fibres gradually diminishing as the muscle extends from one branchiostegal ray to the next.

The muscle extends from the fifth branchiostegal ray on to the medial face of the suboperculum.

Sternohyoideus (SH, Figs 8, 9 & 10). This is a deep narrow muscle, the posterior limits of which are difficult to define. There is an abrupt change of fibre direction and a feeble myoseptum below the leading edge of the cleithral limb which would appear to mark the anterior limit of the body musculature. (In Cynodontini, however, this is not *hypaxial* body musculature but the *abductor superficialis* of the pectoral girdle ; see Figs 9 & 10, also p. 221.)

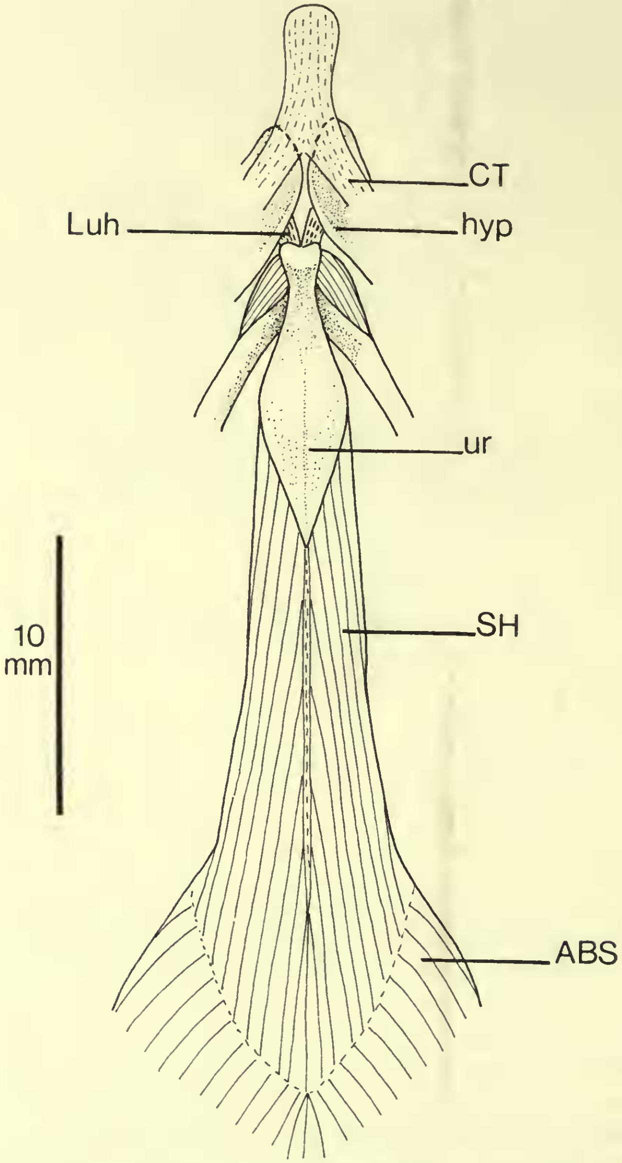

FIG. 9. *Cynodon gibbus*, *sternohyoideus*, ventral view.

In *Rhaphiodon* the myoseptum between the muscle is a more evident barrier than in *Cynodon* or *Hydrolycus*.

Dorsally, the *sternohyoideus* is divided. The dorsal element (SHD, Fig. 10) extends from the anterior edge of the cleithrum to insert principally through a long tendon running to the tip of the urohyal. Laterally, however, some fibres insert directly on to the lateral face of the urohyal. Posteriorly, fibres run into the main ventral mass of the *sternohyoideus*.

Among the characoids this dorsal separation of the muscle appears to be shared only by members of the Characini (p. 232). Winterbottom (1974 : 270) records such an element in gobiids (after Dietz, 1914) and triacanthiids, and applies the name *sternobranchialis* to this muscle. However, I have refrained from identifying this muscle in characoids until a more adequate survey is made of its occurrence in other teleosts and a definite homology thereby established.

The fibres of the main part of the *sternohyoideus* run antero-dorsally to insert upon the lateral face of the urohyal. The entire muscle is very tendinous. No myosepta appear to be differentiated. Ventrally the muscle is delimited by a strong tendon which runs from the posterior edge of the expanded ventral surface of the urohyal.

Muscles of the branchial arches (Fig. 10)

No previous comparative study of the branchial arch musculature in the characoids has been attempted, although Winterbottom (1974) illustrated and commented upon certain aspects of this musculature system in *Brycon guatemalensis* and the dorsal and ventral branchial arch muscles of *Hydrocynus* were described and figured by Kampf (1961).

The arrangement in the Cynodontini is basically as in *Brycon*, and a provisional survey of branchial arch myology in representative species of various characoid families (pers. obs.) suggests relative uniformity throughout the group. However,

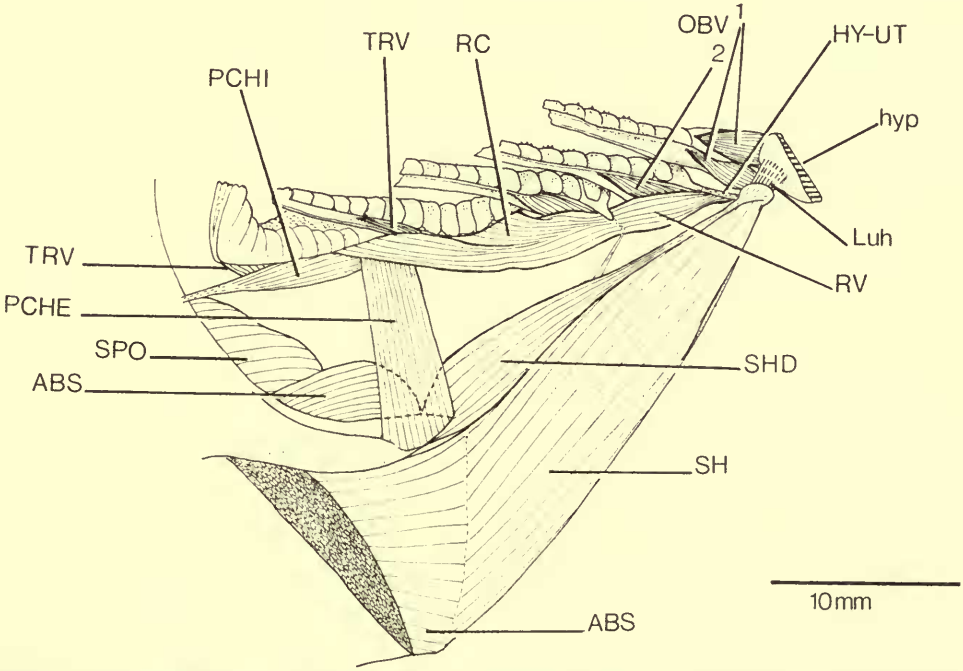

Fig. 10. *Cynodon gibbus*, ventral branchial arch and hyoid musculature, lateral view. The hypohyal has been cut through and moved out of position.

some specializations have been found in those taxa with epibranchial organs (*Chilodus*, *Anodus*).

The following observations were made on the branchial muscles of the Cynodontini.

Obliqui ventrales (OBV1–4, Fig. 10). These are present on the first, second and third gill arches ; that on the first is divided into two elements, one being applied to the leading edge of the ceratobranchial and the hypobranchial, the other placed ventrally.

Rectus ventralis (RV, Fig. 10). This is a thick muscle interconnecting the second and third hypo- and ceratobranchials. The muscle stems from the fascia of tissue which forms a barrier between it and the *rectus communis* (RC). Insertion is into a tendon which runs from the anterior edge of the second hypobranchial to insert into the tip of the urohyal (HY-UT, Fig. 10).

A very thin tendon runs ventrally from the medial surface of the third hypobranchial to pass into the dorsal division of the *sternohyoideus* (see p. 000).

Rectus communis (RC, Fig. 10). This muscle extends from the third hypobranchial to connect with the fourth ceratobranchial and finally to insert along the fifth ceratobranchial.

Transversi ventrales (TRV, Fig. 10). These connect each fourth and fifth ceratobranchials across the midline.

Pharyngoclavicularis externus (PHCE, Fig. 10). This muscle originates from the lower limb of the cleithrum to lie close against the surface of the *abductor superficialis*. It inserts on the fifth ceratobranchial medially to the *rectus communis*.

Pharyngoclavicularis internus (PCHI, Fig. 10). This originates via a long tendon from the anterior edge of the cleithrum and inserts on the fifth ceratobranchial medially to the *rectus communis*.

An examination of the muscles serving the dorsal branchial elements has revealed little difference between the condition in these species and that in *Brycon guatemalensis* as figured and partly described by Winterbottom (1974).

Pectoral Fin Musculature

(Fig. 11)

Although this study is primarily concerned with the cranial muscles, the pectoral muscle system appears to be so extraordinary, and seemingly plays such an important part in the functioning of the jaws (see p. 224), that some elements of the system are described.

In all genera of Cynodontini the coracoids are extensive, thin sheets of bone, closely applied to each other along the midline. Nelson (1949) states that in both his specimens of *Rhaphiodon vulpinus* the major part of the coracoid plate was formed by '. . . one of the coracoid pair, the other being fused to the first proximally' (which I take to mean along the dorsal margin of the bone). I have not found this condition in the specimens of *Rhaphiodon* and *Hydrolycus* I have examined, the two coracoids always being fully developed. It is possible, of course, that such fusion

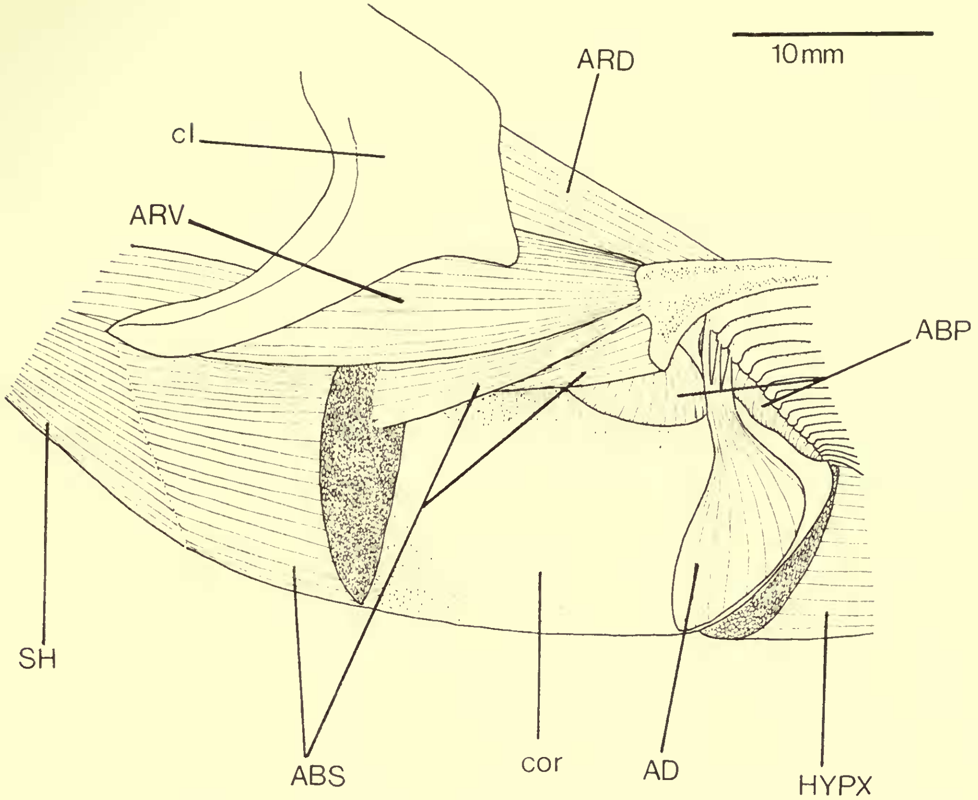

FIG. 11. *Cynodon gibbus*, pectoral fin musculature, left lateral view. The *abductor superficialis* has been cut through leaving intact only those segments that run to the first ray.

occurs in large individuals ; unfortunately, Nelson did not state the size of the specimens at his disposal.

The lateral faces of the coracoids provide sites of origin for the extensive *abductor superficialis* muscle (ABS, Fig. 11) which originates as a thick bundle of fibres curved around the anterior edge of the coracoid.

When the jaws are almost closed this part of the muscle can be seen protruding into the branchial cavity.

Applied to the posterior lateral face of the coracoid and lying medially to the *abductor superficialis* there is a triangular sheet-like muscle. The apex of this element inserts via long tendons on the bases of the second, third and fourth pectoral fin rays (AD, Fig. 11).

This muscle has not previously been described for this tribe (Nelson, 1949) and I have been unable to locate it in any other characoid I have examined. Nor, as far as I am aware, has it been described in other teleosts exhibiting a similar pectoral girdle (i.e. *Pantodon*, *Osteoglossum* ; see Greenwood & Thomson, 1960). The function of this element would appear to be that of a depressor (see below, p. 224). It is perhaps a derivative of the *abductor superficialis*.

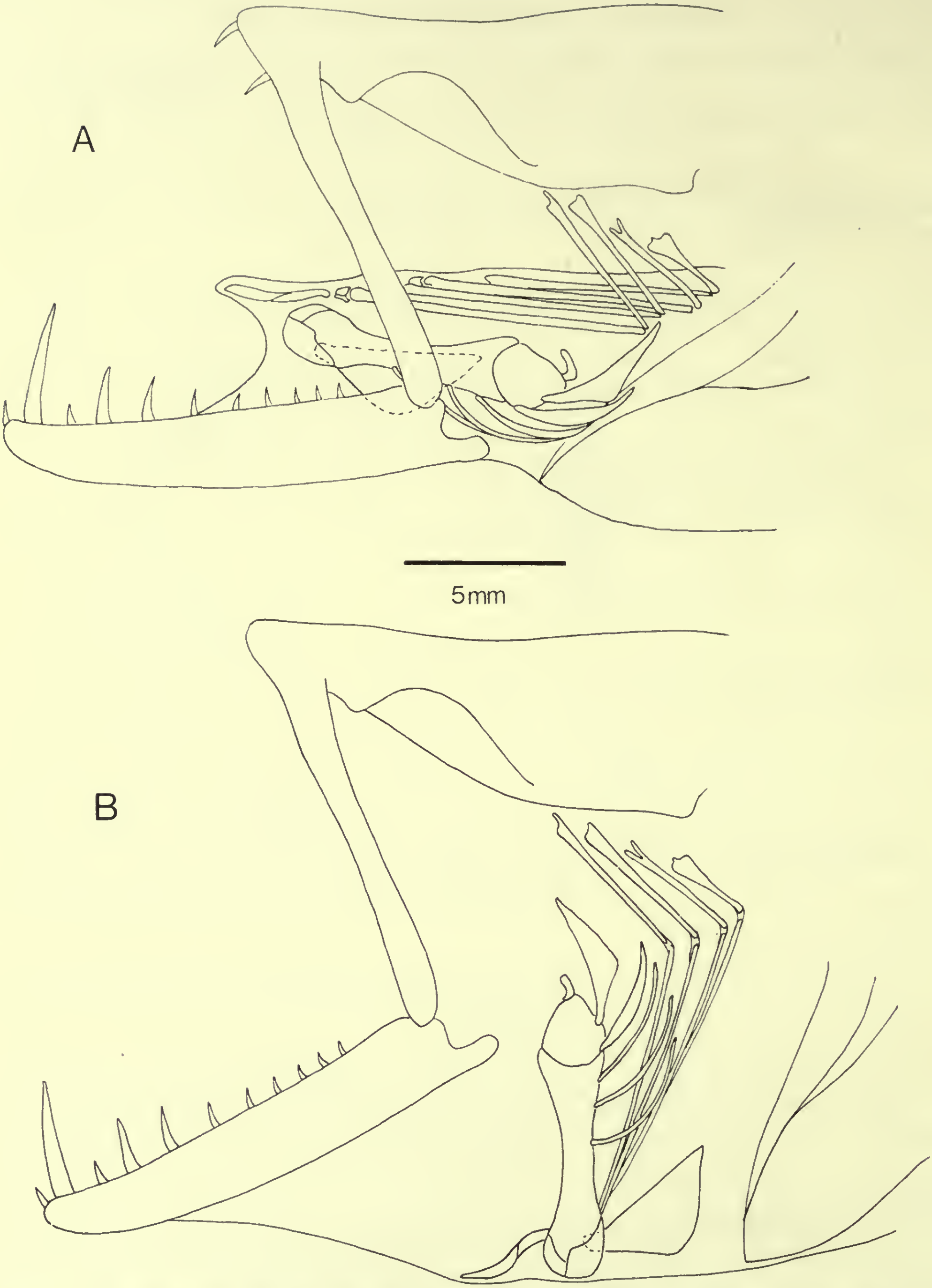

FIG. 12. *Rhaphiodon vulpinus*, outline drawings (made from an alizarin preparation) to show the positions of the hyoid bones when (A) the mouth is half-closed and (B) fully opened. That part of the urohyal obscured by overlying bones is indicated by a dashed line.

Functional Morphology
(Figs 12, 13 & 14)

There do not appear to be any published observations on the feeding behaviour of any members of the Cynodontini. All species seem to be piscivorous; examinations of stomach contents have revealed remains of a characoid (? Hemiodontidae) and cichlids (genera indet.; pers. obs.).

It is of course recognized that the reconstruction of muscle function from the manipulation of preserved material is a hazardous procedure, and that interpretations derived from such observations must be considered highly speculative. Nevertheless, an attempt is made here to reconstruct the possible sequence of movements made by certain parts of the body when the fish (*Rhaphiodon*) is feeding.

In lateral view, the mouth is capable of at least a 90° gape (Fig. 12). The outer surface of the mandibular-suspensorial joint is covered with collagenous tissue. There is a short lateral quadrato-articular ligament embedded within this tissue. Medially there lies a similar ligament (Laq, Fig. 13). From the retro-articular a

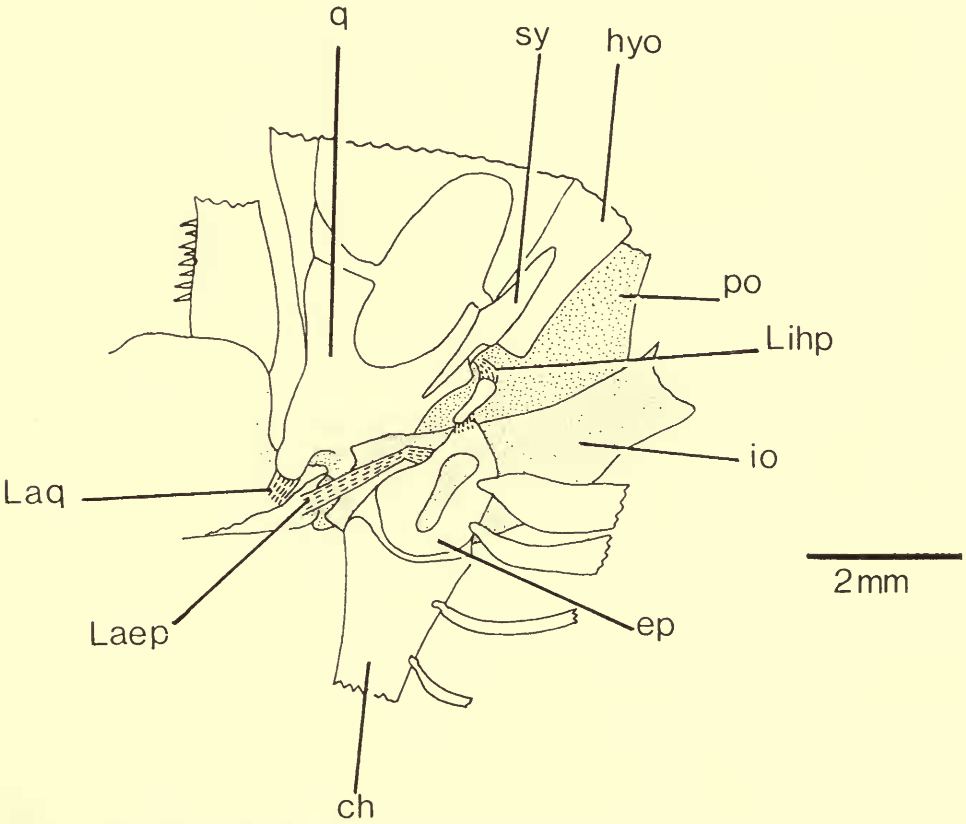

FIG. 13. *Rhaphiodon vulpinus*, ligamentous system of the lower jaw, medial view, right side. The interorbital is indicated by fine stippling, the preoperculum by coarse stippling.

ligament runs dorso-caudally to become applied to the interoperculum. From this point of attachment it is directed somewhat medially to insert upon the lateral face of the epihyal (Laep, Fig. 13). The interhyal is joined by a short ligament to the operculum (Lihp, Fig. 13).

The dentaries are joined at the symphysis by a complexly convoluted hinged joint ('knuckle' joint of Nelson, 1949). Although in preserved material this joint appears to be a rigidly fixed unit, in life no doubt it is capable of allowing the dentaries a substantial degree of lateral movement about this point (Nelson, 1949).

The ligamentous system suggests the capability of an extensive rotation of the dentaries at the quadrate joint and further implies a large abduction of the suspensoria which would force the dentaries widely apart (see Osse, 1969 : 376, concerning observations on the Pike-perch, *Stizostedion*).

A possible sequence in the feeding action may be as follows. As the fish closes upon its prey the mouth is already partly open ; the large pectoral fins are extended laterally, acting as a brake (Nelson, 1949 : 508) ; possibly the small accessory *abductor superficialis* muscle described earlier (p. 221) acts as a depressor and holds the fin rays firmly in position. Contraction of the main *abductor superficialis* and of the ventral *hypaxial* muscles pulls the coracoid ventro-posteriorly and serves to reinforce the contraction of the *sternohyoideus*. The urohyal is moved into a horizontal position (Fig. 12B), the buccal cavity is enlarged by the removal of the hyoid bars into a ventral position ; the 'elastic' connective tissue surrounding the basihyal and extending between the *protractor hyoideus* and the dentaries is everted to form a pouch.

To what degree there is an upward movement of the neurocranium I am unable to ascertain. At rest the skull is aligned in a tilted position to facilitate maximum gape, that is, unlike the situation in the superficially similar stomiatoid *Chauliodus* described by Tchernavin (1953), where there is some considerable upward movement of the cranium into a suitably inclined position when the fish 'strikes' its prey. Strong tendinous attachments of the *epaxial* musculature to posterior parts of the cranium and the development and arrangement of many long intermuscular bones suggest some degree of movement. In *Rhaphiodon* numerous intermuscular bones (*c.* 80–90) are arranged in the *epaxialis* (imb, Fig. 14). The bones are aligned at angles of between 10° and 20° to the horizontal. Their dorsal ends are split into three or four branches. The epaxial muscle fibres are arranged at similar angles but in the opposite direction. Anteriorly the intermuscular bones lie almost horizontal to the body axis and they stem as a bundle from the pterotic.

A further series of Y-shaped bones (epineurals) are found arranged along the bases of the neural spines and embedded in the *lateralis superficialis* (LAT.S, Fig. 14). This latter muscle is a discrete, thick band well separated dorsally from the *epaxialis*. The outer layers of fibres are arranged horizontally, the deeper layers are aligned diagonally. Ventrally, the muscle is not clearly differentiated from the hypaxial body musculature.

Neither *Cynodon* nor *Hydrolycus* display such a marked differentiation of the *epaxialis* from the *lateralis superficialis* as is seen in *Rhaphiodon*, and neither do they possess the numerous intermuscular bones of the *epaxialis*.

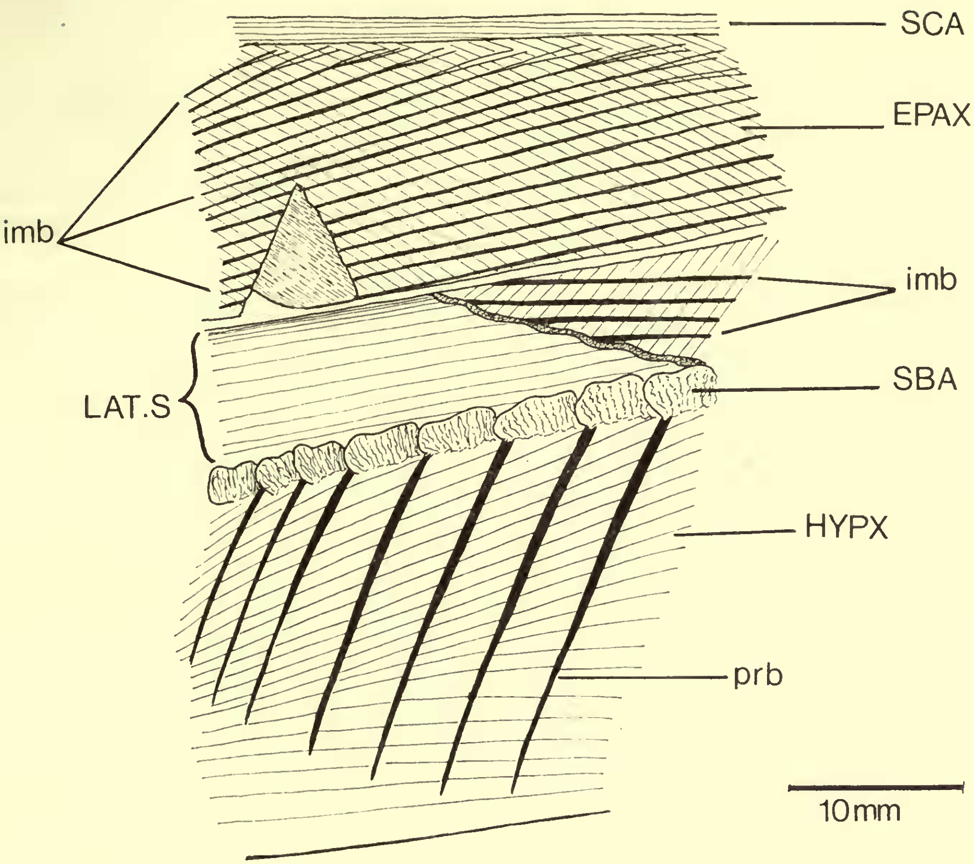

FIG. 14. *Rhaphiodon vulpinus*, section through the anterior body musculature showing the orientation of the intermuscular bones. Part of the *epaxialis* has been cut away to show the medial orientation of the fibres. All bones are shown in solid black.

In all three genera supraneural (predorsal) bones are numerous (*c.* 18–20); in *Rhaphiodon* they are reduced to slender rods.

The arrangement of the body musculature and intermuscular bony elements in *Rhaphiodon* obviously serves to counteract stresses from forces being applied anteriorly and along the dorsal surface of the body, such as might be produced by a dorso-posterior movement of the cranium.

The sabre-like canine teeth may serve as a trap to retain the prey in the mouth rather than as a means of impaling it. Removal of an impaled fish would be difficult and would require rapid movement of the jaws. It is likely that the fish relies on a suction method of feeding by rapidly activating the opercular mechanism (Alexander, 1967).

The narrow head affords a wide angle of vision which would certainly be stereoscopic anteriorly, ventrally and dorso-anteriorly.

Taxonomic Considerations

The status of the genus Roestes *Günther, 1864* (Figs 1D & 15)

The genus *Roestes* has been considered a member of the Characinae (*sensu* Eigenmann, 1909, 1910). Gery & Vu (1963) commented upon the similarities between this genus and *Hydrolycus*, remarking '. . . Il n'est pas impossible que *Roestes* fasse la jonction entre les Characinae et les Raphiodontinae'. Menezes (1974) revised the genus and included the following taxa in synonymy: *Lycodon*, *Gilbertella*, *Gilbertolus* and *Xiphocharax*.

Although Menezes presented an osteological description this was not complete, covering only the dermal cranial bones. From his study he concluded that *Roestes* was related to *Heterocharax* but that it did not belong to the same tribe as that genus, namely the Heterocharacini (see p. 234 for a discussion of this taxon).

My observations suggest that *Roestes* is not related to *Heterocharax* and furthermore that it is not even a member of the Characini but should be placed in the tribe Cynodontini on the basis of the following specialized characters shared with that group:

Adductor mandibulae section A_1 reduced (i.e. it does not extend along the ventral border of A_2 as in Characini);

Adductor mandibulae section A_2 is divided by the *levator arcus palatini* (never divided in the Characini);

Levator arcus palatini confined to the dorsal part of the hyomandibula (in the Characini the muscle extends ventrally along the anterior border of the bone);

Pectoral fin musculature is highly developed. The *abductor superficialis* is not separated from the *sternohyoideus* by the cleithrum as in the Characini; the accessory *abductor* muscle described in the Cynodontini (p. 221) is present.

Other, non-myological, characters are:

Teeth are arranged in a single series in both jaws (two rows present in either, or both, jaws in Characini, but with one exception, see p. 237);

The *coracoids* are extensively developed, extending far anteriorly and are joined medially along their entire midlines (in Characini the coracoids are only moderately developed and diverge posteriorly);

Pectoral fins are long, rays numbering I 17 (cf. I 12–15 in Characini);

Branchiostegal rays are five (four in Characini).

The skull displays no specialized characters which could be considered as essentially cynodontine or characinine. The dilatator fossa is moderately developed as in most Characini. A rhinosphenoid is present and the orbitosphenoid is widely separated from the parasphenoid; both features appear to be plesiomorph for the Characidae.

The hyomandibula is similar in form to that bone in the Characini.

Two other osteological characters which are noted in *Roestes* are the possession of well-developed intermuscular bones originating from the pterotic and a relatively high number of supraneural (predorsal) bones.

Cranially originating intermuscular bones appear to be a specialization amongst the characoids. Apart from the Cynodontini I have found them only in the Ctenoluciidae.

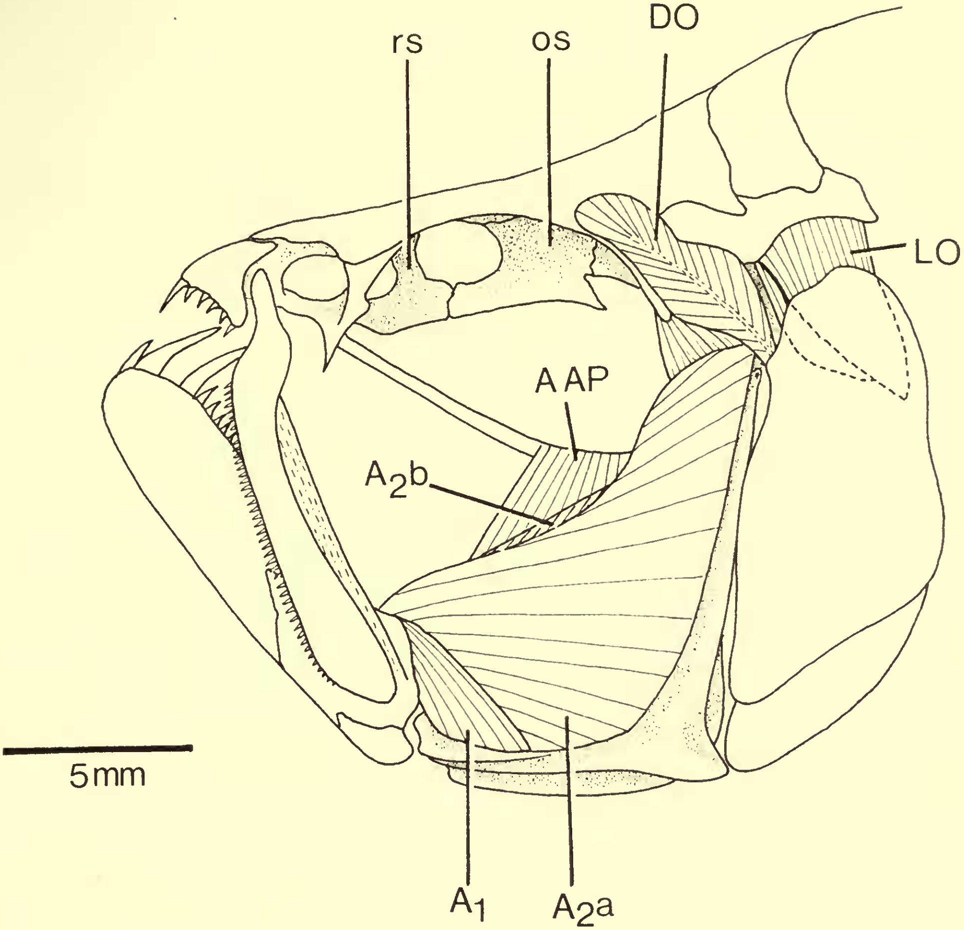

FIG. 15. *Roestes alatus*, superficial facial musculature, lateral view. The dashed lines on the operculum show the extent of the *levator* and *adductor operculi.*

The number of supraneurals varies considerably and appears in part to be correlated with the elongation of the body. In the Cynodontini they number 18–20, in the Characini never more than 5, in *Roestes* 8–9. Although in number this is closer to the Characini, *Roestes* is a relatively deep-bodied fish as compared with the characinine *Cynopotamus* and in this case the increased number does not seem to be a correlate of elongation (although it may reflect different stresses placed upon the dorsal surface of the body, see p. 225).

Intrarelationships of the Cynodontini

A combination of the following specialized characters is shared by all members of the Cynodontini :

Adductor mandibulae A_1 reduced to a small slip of muscle. A_2 is complexly pinnate with several origins ; it is divided by the *levator arcus palatini* ;

Dilatator operculi origin from both the dorsal and ventral surfaces of the frontals (except in *Roestes* where origin is entirely from the dorsal surface) ;

Levator operculi origin in part from the tendon of the *lateralis superficialis* and in part from the supracleithrum ;

Sternohyoideus dorsally divided ;

Pectoral fin musculature extensively developed, the *abductor superficialis* being virtually continuous with the *sternohyoideus* (i.e. not separated by the cleithrum), and an accessory *abductor* muscle present ;

First obliqui ventrales divided ;

Non-myological specializations are :

Branchiostegal rays number five, the first three spathiform, the two posterior ones acinaciform ;

Hyomandibular bone modified (except in *Roestes*) ;

Coracoids extensive, closely applied or fused ;

Sphenotic process well developed, sometimes laterally extended ;

Intermuscular bones originating from the posterior of the cranium.

Although none of the non-myological characters (with the exception perhaps of the modified hyomandibular bones) is confined to the Cynodontini, no other characoid is known to possess more than three of these in combination.

It would seem that there are two groups of species constituting the Cynodontini.

1. *Rhaphiodon* and *Cynodon* are characterized by having depressed crania, stout horizontal parasphenoids articulating with the orbitosphenoids and prominent laterally directed sphenotic processes.

It is difficult to say which of these two genera is more highly specialized. Nelson (1949) showed that the swimbladder in *Rhaphiodon* was of a complex structure possessing numerous appendices, some of which penetrate the body wall (SBA, Fig. 14). In *Cynodon* (and other cynodontine genera) the swimbladder does not appear to be specialized in this way. It is shorter than that found in *Rhaphiodon*, extending to just past the origin of the anal fin, and there are no appendices in contact with the body wall (although in *Roestes* the *tunica externa* is closely applied to the body wall).

In *Cynodon* the rhinosphenoid is absent, a feature perhaps correlated with the depression and elongation of the skull.

2. *Hydrolycus* and *Roestes* are characterized by a rather more vaulted cranium, a curved parasphenoid well separated from the orbitosphenoid, and narrow, posteriorly directed sphenotic processes.

Roestes differs from all other cynodontine genera in lacking the highly specialized development of the *adductor mandibulae* A_2 and *dilatator operculi*. Also absent is the modified hyomandibula.

The genus *Roestes* appears to occupy something of an intermediate position between the Characini and Cynodontini and is possibly the most primitive extant representative of the tribe.

The possible phyletic relationships of the tribe Cynodontini are shown in Fig. 21.

Tribe **CHARACINI** Fowler, 1958

Characidi Fowler, 1958
Characinae Eigenmann, 1909

The Characinae was erected by Eigenmann (1909; genera enumerated, 1910) to contain the following genera: *Charax* Scopoli, *Roestes* Günther, *Gilbertolus* Eig., *Roeboides* Günther, *Bramocharax* Gill, *Eucynopotamus* Fowler, *Evermannolus* Eig.,

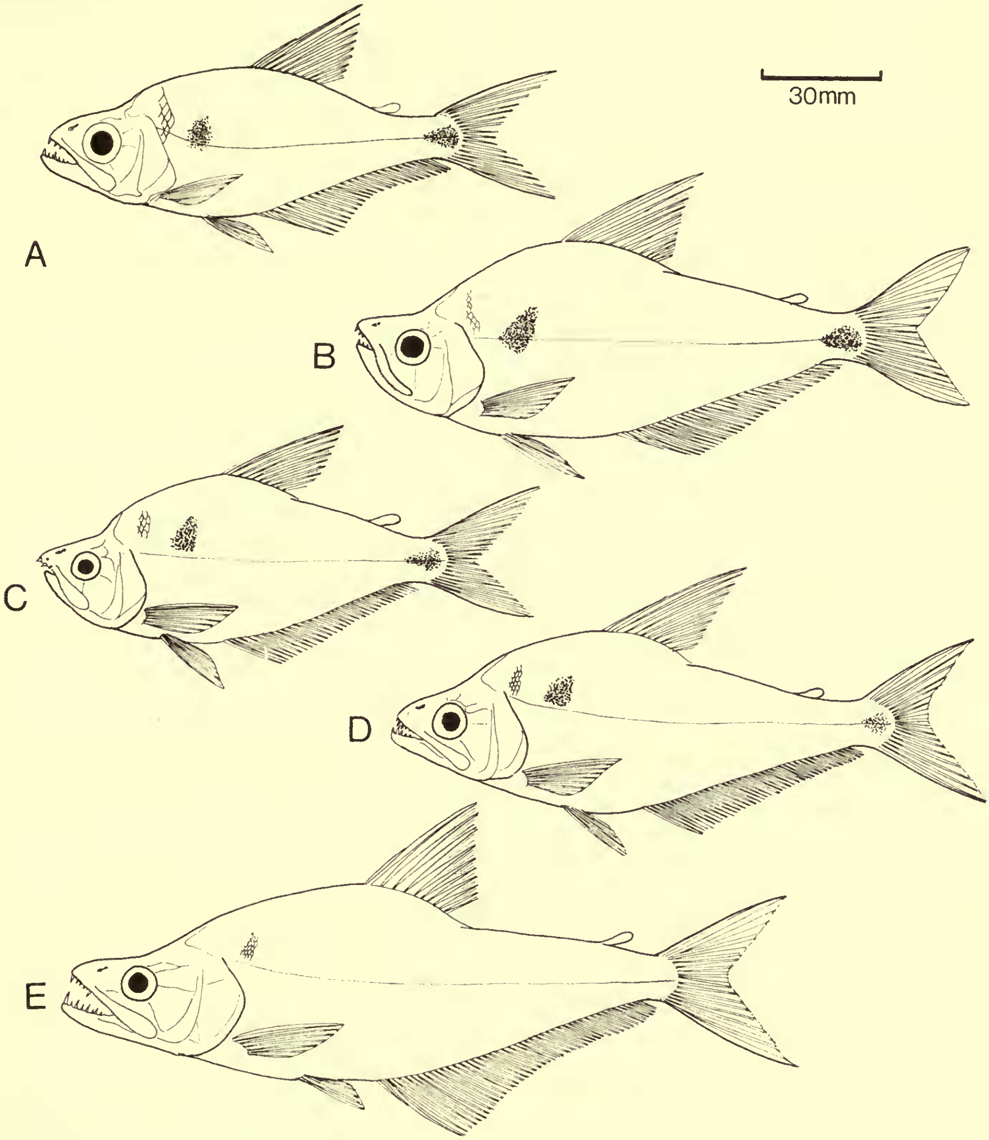

Fig. 16. Outline drawings of (A) *Acanthocharax microlepis*, (B) *Charax gibbosus*, (C) *Roeboides dayi*, (D) *Cynopotamus* (*Hybocharax*) *magdalenae* and (E) *Cynopotamus* (*Cynopotamus*) *argenteus*. All drawn to scale.

Asiphonichthys Cope, *Salminus* Agassiz, *Catabasis* Eig. & Norris and *Exodon* Müller & Troschel (*Cynopotamus* Val. was considered a synonym of *Charax*).

Later, Eigenmann (1912a) included *Acanthocharax* and *Heterocharax*. Subsequent authors have added other genera, including *Cyrtocharax* Fowler, 1906; *Genycharax* Eig., 1912; *Gnathocharax* Fowler, 1913; *Lonchogenys* Myers, 1927; *Moralesia* Fowler, 1943; *Roeboexodon* Gery, 1959; and *Hoplocharax* Gery, 1966. This list does not include those genera considered to be synonyms of any of the above taxa.

The inclusion of these genera in the tribe on the basis of shared specialized myological characters is discussed on pp. 233–238. *Charax gibbosus* forms the basis for the following description of the cranial musculature.

Description of the Cranial Musculature of *Charax gibbosus* (Linn.)

(Fig. 16B)

Facial musculature (Fig. 17)

Adductor mandibulae section A_1. This is a small element lying at an angle of 45°. It originates posteriorly from the preoperculum and the ventral edge of the quadrate to insert along the dorsal edge of the angulo-articular.

Extending from this insertion is the extensive connective tissue band which joins the maxillary to the lower jaw. As in the Cynodontini the '*ligamentum primordiale*' is in fact a thickening of the folded tissue that forms the floor of the orbital cavity. Posteriorly, however, the tissue does become differentiated into a 'ligament' which passes laterally to A_1 and is attached to the outer face of the angulo-articular. (This condition is found throughout the Characini, the folded skin enabling the maxillary to move well forward when the mouth opens.)

Section A_2 originates dorsally and medially from the hyomandibula and posteriorly from the preoperculum. Ventrally a strong tendon runs from the quadrato-preopercular region to join the aponeurosis of the *adductor mandibulae* at the jaw articulation.

The aponeurotic sheet is a small triangular area, the ventrally directed apex of which gives rise to the stout tendon that forms the posterior border of A_w.

Section A_w fills the coronomecklian cavity. It is a bipinnate muscle, the midline raphe stretching to a point halfway along its length.

Levator arcus palatini. This muscle extends from the ventral surface of the sphenotic process to insert upon the hyomandibula. In some specimens, fibres extend also from the ventral surface of the frontal.

Adductor arcus palatini. This is a short element confined to the posterior section of the parasphenoid. Insertion is upon the metapterygoid and hyomandibula.

Dilatator operculi. This muscle takes its origin from the fossa formed by the frontal and sphenotic, and also from the lateral border of the pterotic; dorsally the pterotic border (at the anterior termination of the pterotic canal) forms a strong indentation in the muscle. Insertion is via a short thick tendon on to the medial face of the anterior opercular process.

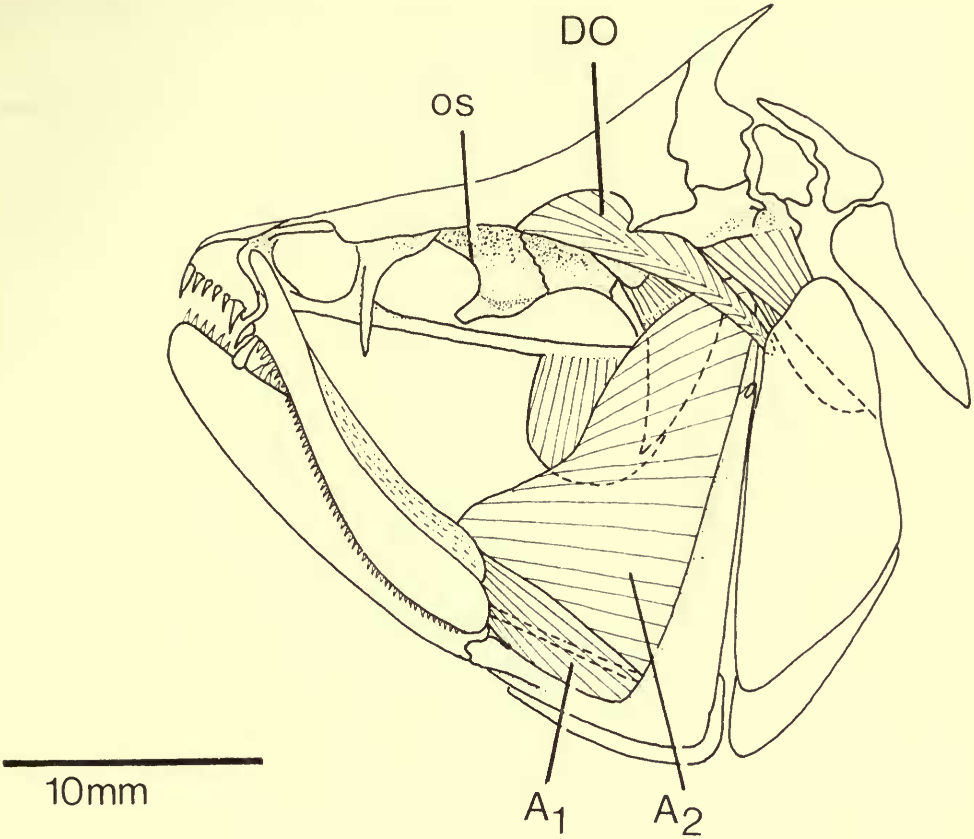

FIG. 17. *Charax gibbosus,* superficial facial musculature, lateral view. The dashed lines indicate the borders of the *adductor arcus palatini, levator arcus palatini, levator* and *adductor operculi.* The dashed lines across *adductor mandibulae* A_1 show the position of the underlying tendon which is the ventral border of A_2.

Levator and *adductor operculi.* The *levator* is a triangular muscle, whose base extends along the lateral border of the pterotic, and the apex inserts along the posterior medial surface of the operculum. The *adductor* stems from a shallow subtemporal fossa and inserts anteriorly to the *levator.*

Hyoid musculature (Fig. 18)

Protractor hyoidei. This extends from the second and third branchiostegal rays to run over the first ray and the ceratohyal. The elements of each side unite into a single short medial section which inserts dorsally and ventrally to the *intermandibularis.*

Hyohyoidei. These are weakly developed (see p. 216). The 'abductores' sections run from the first branchiostegal rays to the hypohyals. As in the Cynodontini, the hypohyals are covered by a connective tissue fascia which extends dorsally to cover the basihyal.

The 'adductores' parts of the muscle are extremely thin, only a single layer of fibres running between the branchiostegal rays.

Sternohyoideus (SH, SHD, Fig. 18). This is a deep muscle taking its origin entirely from the cleithrum and inserting along the lateral face of the compressed urohyal. Dorso-laterally the muscle is divided (as in the Cynodontini). The insertion of the dorsal division is via a long tendon on to the third hypobranchial. Prior to insertion the tendon is joined by its fellow from the opposite side, the two becoming firmly united along the midline before diverging to their respective insertions.

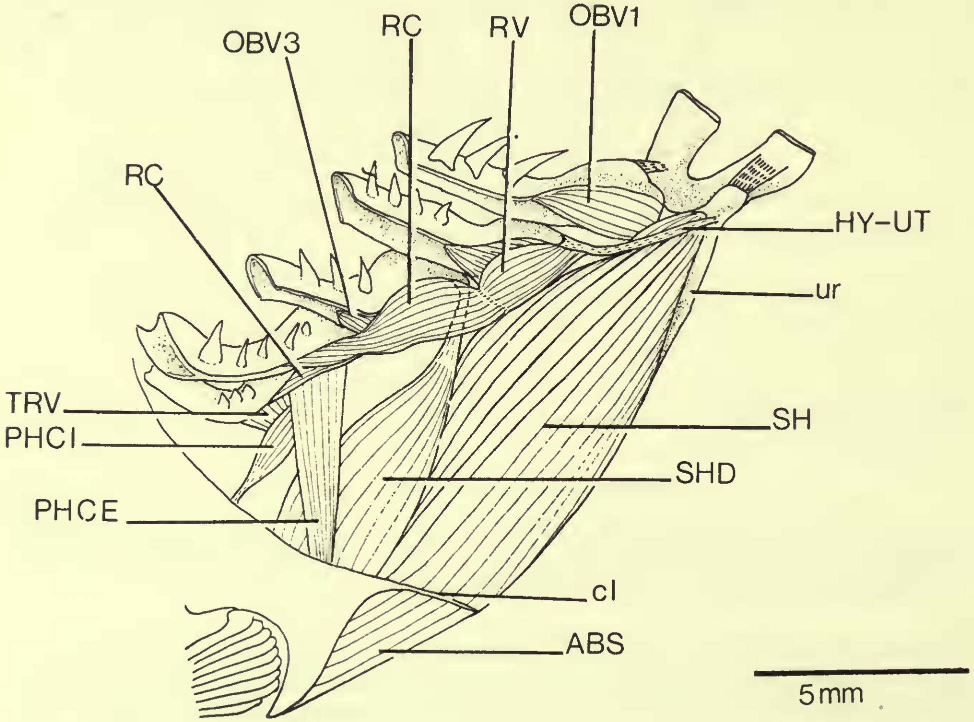

Fig. 18. *Charax gibbosus*, ventral branchial arch and hyoid musculature, lateral view.

A similar tendon is present in the Cynodontini (Fig. 10) although it is not as strongly developed. Nor, in that tribe, does it serve as the insertion tendon for the dorsal division of the *sternohyoideus*. A similar tendon is present in other characoids. I have observed it in *Brycon falcatus*, *Hoplias malabaricus* and *Acestrorhynchus* species.

Dietz (1914) refers to a similar tendon being present in *Gobius*. (See also Winterbottom, 1974 concerning the *sternobranchialis* ; also fig. 27 in that work illustrating a ventral tendon in *Elops*.)

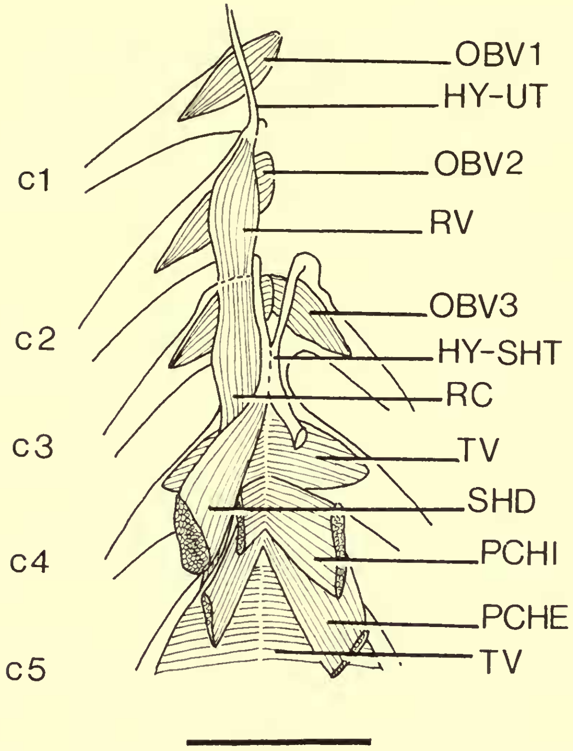

FIG. 19. *Charax gibbosus*, ventral branchial arch musculature, ventral view. Some of the elements have been cut through or removed.

Muscles of the branchial arches (Figs 18 & 19)

The arrangement is similar to that described for the Cynodontini.

Rectus ventralis (RV). This is bordered anteriorly by a long tendon which runs from the second hypobranchial to insert upon the urohyal (HY-UT).

Rectus communis (RC). This is very short and thick, extending from the third hypobranchial to insert on the fourth and fifth ceratobranchials.

Obliqui ventrales (OBV 1–3). These are well developed. OBV 1 shows something of a medial division but is not completely divided as in the Cynodontini.

Taxonomic Considerations

The genera of the Characini

There is much confusion concerning the taxonomy of the genera and species assigned to the Characini (Characinae *sensu* Eigenmann ; see Schultz, 1950 ; Gery, 1972a ; Gery & Vu, 1963). The assortment of genera listed above (p. 229) does not, in my opinion, constitute a monophyletic assemblage and on these grounds some genera should be excluded from the Characini as here defined. A review of these genera shows the current status of the taxa to be as follows.

Roestes. Elsewhere in this paper (p. 226) reasons have been given for including this genus in the Cynodontini.

Gilbertolus. This is a synonym of *Roestes* (see Menezes, 1974).

Bramocharax. This is a tetragonopterine, possibly related to *Astyanax.* The species have been described and the genus discussed by Rosen (1970, 1972).

Eucynopotamus. This has been considered a subgenus of *Charax* by Gery & Vu (1963). Due to lack of material I have been unable to assess the validity of 'subgenera' within the *Charax* group.

Evermannolus. This is a synonym of *Eucynopotamus* (see Schultz, 1950 ; Gery & Vu, 1963).

Salminus. This genus is certainly not related to any of the genera here included in the Characini. Myologically it is specialized (pers. obs.) and would appear to be related to the Bryconini–Tetragonopterini lineage (see also remarks on interrelationships by Roberts, 1969 : 435–7).

Catabasis. This genus is known only from the holotype of *C. acuminatus* and is considered by Roberts (1969 : 438) to be '. . . a distinct genus of Characidae'. Its status cannot be assessed until further material comes to hand.

Exodon. Superficially this genus resembles *Roeboides,* possessing external teeth along the upper jaw. However, the cranial musculature is that of a tetragonopterine or bryconine fish (pers. obs.).

Gery (1959) considered that *Exodon* together with *Roeboexodon* constitute part of a lineage, including *Holobrycon* (*Brycon*), which is related to *Roeboides.* Purely on myological grounds I do not believe that *Exodon* is related to *Roeboides* and I can find no evidence to suggest that it belongs to the Characini. Its true relationships may become apparent after detailed osteological study.

Heterocharax, Lonchogenys and *Hoplocharax.* Gery (1966) established a 'subtribe', the Heterocharacini, to contain these three monotypic genera.

Apart from the conical dentition, *Heterocharax macrolepis* shares none of the specialized features associated with the Characini. The cranial musculature is typically that of a tetragonopterine (i.e. large *adductor mandibulae* A_1 indistinctly separated from A_2 posteriorly ; *dilatator operculi* restricted to a small, laterally situated sphenotic fossa ; *sternohyoideus* undivided and originating from the cleithrum). The coracoids are small and widely divergent posteriorly. The orbitosphenoid is reduced ; a rhinosphenoid is present.

I have been unable to examine specimens of *Lonchogenys* or *Hoplocharax.*

Gery (1966) considered that this subtribe was '. . . still rather close to the generalized tetragonopterine type'. I would agree with this statement and for the present the phyletic position of the 'subtribe' Heterocharacini must remain uncertain but it can be excluded from the Characini.

Gnathocharax. Eigenmann (1916) suggested that this genus was closely related to *Roestes* (cited as *Gilbertolus* in that paper). This view was endorsed by Böhlke (1955) who stated : 'The characteristics shared by the two genera are overwhelming and their common ancestry seems certain.' In its general morphology *Gnathocharax* certainly does resemble *Roestes,* particularly in possessing elongate pectoral fins. It shares also the expanded coracoids which are closely applied along the midline. However, the lower jaw is shallow, and the dentition is of a rather different pattern (features shared with *Heterocharax*). Again, the cranial musculature is of the tetragonopterine type and the hyoid muscles show none of the specializations of the Characini.

I find this genus something of a problem : certainly there are no myological features that would place it unequivocally in the Characini or the Cynodontini. As far as I can see osteologically it greatly resembles *Heterocharax*, apart from the development of the coracoids (which is probably a parallel of this character in *Roestes*). For the moment I would suggest that *Gnathocharax* be included within the 'Heterocharacini'.

Genycharax. This monotypic genus Eigenmann (1912b) related to '... the Tetragonopterinae on the one hand and to *Exodon* on the other'.

Miles (1947) placed the genus in the Characinae (Characini in this paper).

The teeth are conical, those forming the outer row on the premaxilla (numbering 12–16) are directed forwards, those on the inner row are curved inwardly, as are those in the lower jaw.

The only specimen I have been able to examine is badly preserved and I am unable to determine whether the *adductor mandibulae* A_1 is reduced to the same degree as in the Characini (see below). There is, however, a dorsal division of the *sternohyoideus* which is a specialization shared with that tribe. The *dilatator operculi* occupies a small fossa.

I have refrained from assigning this genus to the Characini until more material is available.

Genycharax tarpon appears to be confined to the Cauca river of Colombia.

The remaining genera to be considered from those listed on p. 230 are *Charax*, *Roeboides*, *Acanthocharax*, *Cyrtocharax*, *Cynopotamus*, *Moralesia* and *Asiphonichthys*.

By virtue of the following shared myological specializations these taxa are considered to constitute the tribe Characini.

The *adductor mandibulae* section A_1 is reduced and is completely separated from A_2, extending along the entire ventral border of that element. In Tetragonopterini and Bryconini it is large and posteriorly the fibres are confluent with those of A_2.

The *levator arcus palatini* sometimes originates from the ventral surface of the frontal. This condition has not been found in Tetragonopterini or Bryconini.

The *dilatator operculi* is long and sometimes extends far on to the dorsal cranial surface. In Tetragonopterini this muscle is always confined to a small laterally placed fronto-sphenotic fossa. It may, however, be found to extend well forward in some species currently placed in the genus *Brycon* (pers. obs.).

A dorsal division of the *sternohyoideus* is present and inserts, via a tendon, on the leading edge of the third hypobranchial. Apart from the Cynodontini, no such division of this muscle has so far been found in any other group of characoids.

Charax and *Roeboides*. Myologically, *Charax* most closely resembles *Roeboides* (cf. Figs 17 & 20B). In both genera the *dilatatores operculorum* run from a shallow fossa (which is strongly indented by the anterior border of the pterotic canal and by the parietal) formed by the frontal and sphenotic. In *Roeboides* (*guatemalensis*, *prognathus* and *myersii*), however, the sphenotic extends further laterally.

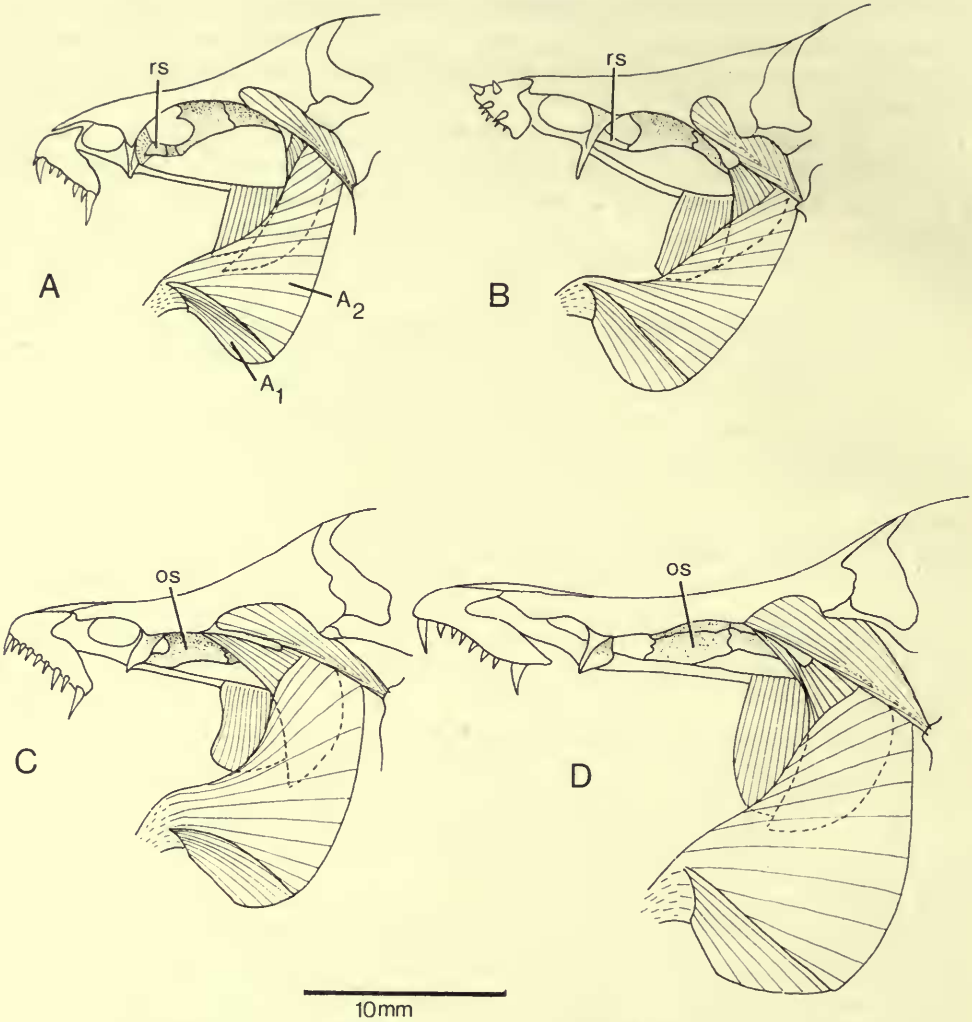

FIG. 20. Superficial facial musculature of (A) *Acanthocharax microlepis*, (B) *Roeboides prognathus*, (C) *Cynopotamus* (*Hybocharax*) *magdalenae* and (D) *Cynopotamus* (*Cynopotamus*) *argenteus*. The dashed lines indicate the borders of the *levatores* and *adductores arcus palatini*.

The *levator arcus palatini* is developed to about the same degree in both genera.

The tendon running from the dorsal division of the *sternohyoideus* to the third hypobranchial is strongly developed.

At this point some mention should be made of certain osteological features which to my knowledge have not been recorded for these genera.

In *Charax* the rhinosphenoid is absent. The orbitosphenoid is in close contact with the parasphenoid. In a series of eleven specimens of *Charax gibbosus* ranging in size from 103 to 70 mm S.L. the degree of contact between the orbitosphenoid and parasphenoid varied, from being narrowly separated to completely united; the degree of separation does not appear to depend on the size of the specimen. This feature (which is also seen in *Cynopotamus*) conflicts with one of the criteria used by Weitzman (1962 : 48) in defining the subfamily Characinae, namely, that the orbitosphenoid is not directly articulated with the parasphenoid. I would consider that such a feature is a specialization correlated with elongation and depression of the skull (a similar situation occurs in *Cynodon* where the orbitosphenoid and parasphenoid are in contact and the rhinosphenoid is absent, see p. 228).

In *Roeboides prognathus* (Fig. 20B) and *R. guatemalensis* the rhinosphenoid is well developed and extends anteriorly of the orbitosphenoid. In *Roeboides myersii*, however, it appears to be absent.

Moralesia. I have been unable to examine any specimens of species belonging to this genus. This taxon has been considered by Böhlke (1958 : 70) to be a distinct genus related to *Charax*. Gery & Vu (1963) consider it a subgenus. Whatever the rank accorded to this taxon, it does appear to belong to the Characini.

Cynopotamus (Figs 16D & E and 20C & D). Gery & Vu (1963) divided this genus into several subgenera. I have examined species representing all these taxa, namely, *C.* (*Cynopotamus*) *argenteus*, *C.* (*Cynopotamus*) *limaesquamis*, *C.* (*Hybocharax*) *magdalenae* and *C.* (*Acestrocephalus*) *goeldii*.

All these species display a long *dilatator operculi*, the fibres of which are shallowly bipinnate. In *C.* (*Cynopotamus*) *argenteus* some ventral fibres of this muscle take their origin from the sphenotic process (a condition also encountered in *Hydrolycus* of the Cynodontini, see p. 215). The form of the dilatator fossa differs somewhat between the subgenera. In *C.* (*Hybocharax*) *magdalenae* the shelf formed by the frontal and sphenotic is posteriorly directed, whereas in *C.* (*Cynopotamus*) *argenteus* and *C.* (*Acestrocephalus*) *goeldii* it is somewhat laterally extended (cf. Figs 20C & D).

In all species examined the dorsal division of the *sternohyoideus* is well differentiated and extends via a long thick tendon to its insertion on the third hypobranchial.

The branchial muscles show something of a modification from those in *Charax* and *Roeboides*. The *obliqui ventrales* are thin and compressed as is the *rectus ventralis* and *rectus communis*. The division between these two elements is not effected by the interface of connective tissue, and the ventral fibres of the *rectus communis* appear to be continuous with those of the *rectus ventralis*.

The median ethmoid of *Cynopotamus* (*Cynopotamus*) *argenteus* is extended and the skull is greatly depressed anteriorly.

Cyrtocharax. This is a synonym of *Cynopotamus* (see Gery & Vu, 1963).

Asiphonichthys. This genus differs from all others here placed in the Characini in possessing a single row of teeth in both jaws. I have only a single specimen of *A. stenopterus* available, and unfortunately its mouth has been damaged. However, the larger canines in the upper and lower jaws appear to be placed slightly medial to the other close-set teeth, as indeed do some of the more posterior teeth.

As far as I can see, there are no other characters, osteological or myological, which would suggest that this genus is other than a member of the Characini.

Acanthocharax (Figs 16B & 20A). This monotypic genus exhibits a more 'generalized' appearance than do any of the other taxa included in this group. The jaws are not so obliquely aligned, the mandibular teeth are numerous and slightly curved ; the body shape does not display a marked gibbosity and there is no ventral keel.

The principal myological differences are again seen in the form of the *dilatator operculi* and its accommodating fossa. The muscle is long, almost unipinnate, and the shelf on the sphenotic is posteriorly directed.

The *levator arcus palatini* is reduced antero-posteriorly and its crescentic lower border extends further ventrally on to the face of the hyomandibula than it does in the other genera examined.

The dorsal division of the *sternohyoideus* is present, inserting through short tendons on to the third hypobranchial.

The parasphenoid is somewhat curved (as in most tetragonopterines and bryconines) and is widely separated from the orbitosphenoid. The rhinosphenoid is well developed and extends anteriorly from the orbitosphenoid, to which it is attached by a band of ligamentous tissue.

Interrelationships of the Characini

Gery (1959) sought to establish a relationship between the characinine *Cyrtocharax* (= *Cynopotamus*) and *Acestrorhynchus* (Acestrorhynchinae). I can find little to substantiate this view. The conical dentition is probably a primitive character for these genera, and the predatory facies is most likely a case of parallelism (see p. 240). However, there are no shared characters which could be termed specialized. In both myological and osteological features *Acestrorhynchus* differs considerably from any member of the Characini. Work is in preparation to establish the nature of its relationship with other characoid taxa.

Of the groups of species recognized as subgenera by Gery & Vu (1963), *Cynopotamus* and *Acestrocephalus* seem to be the most extreme and represent the specialized predator lineage of the tribe, which has possibly been derived from the basal *Charax–Roeboides* ancestral group.

Just how closely related are *Charax* and *Roeboides* is difficult to say. They certainly resemble each other in their muscle morphology, but these resemblances are plesiomorphic for the Characinae. No comparative osteological studies of these genera have been made and those undertaken in the course of this study have been rather limited. For the moment I would suggest that *Charax* and *Roeboides* are more closely related than are either to any other taxon within the Characini.

I am treating *Acanthocharax* as the representative of the plesiomorph lineage of this group. This is mainly on the basis of the 'generalized tetragonopterine' skull and relatively unspecialized dentition.

Because of lack of material I have been unable to place the genera *Moralesia* and *Asiphonichthys*. *Moralesia* would certainly seem to be closely related to *Charax* (see p. 237) ; the relationships of *Asiphonichthys*, however, are rather more obscure. It is the only genus of the Characini to possess a single row of teeth in both jaws (p. 237) ; whether this is a primitive or a derived condition for the Characinae is

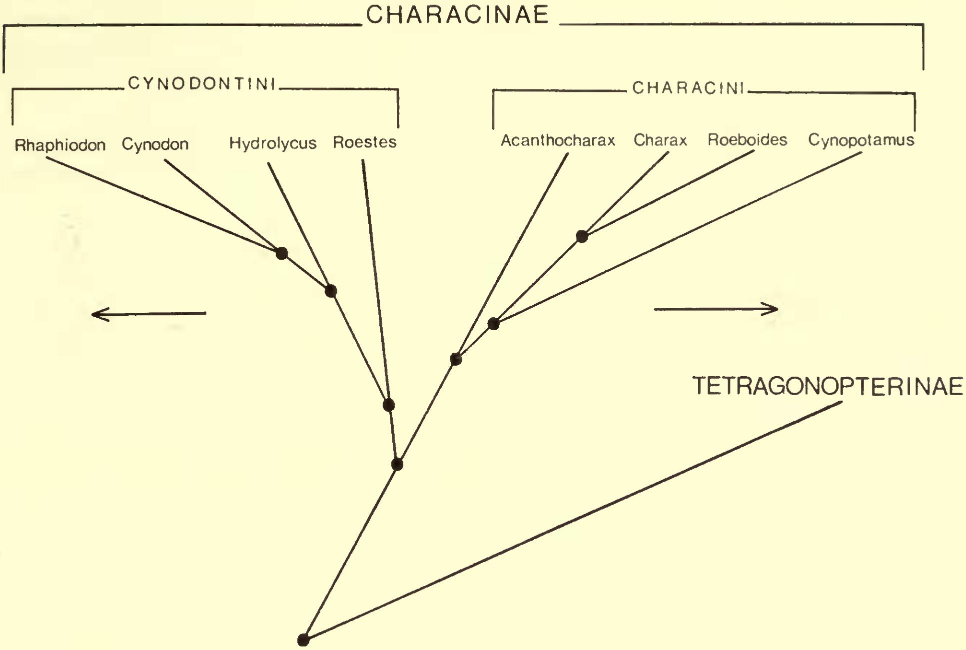

FIG. 21. Cladogram of the Characinae. The arrows indicate the trends toward elongation of the body, increase in the number of body scales, lengthening of the anal fin and development of specialized dentition. The positions of the genera *Asiphonichthys* and *Moralesia* are not indicated (see pp. 237–238).

not known at present. *Asiphonichthys* is probably a derivative from the *Charax–Roeboides* lineage.

The specialized myological features found in all Characini and shared with all Cynodontini are the reduced *adductor mandibulae* section A_1 and the divided *sternohyoideus*. These are not, as far as I know, found in other characoid taxa.

I would consider the Cynodontini and Characini to be sister tribes, together forming the subfamily Characinae. The Characinae in turn is the sister group of the Tetragonopterinae (= Characinae of Weitzman, 1962).

Remarks on the genus Agoniates *Müller & Troschel, 1845*

The genus *Agoniates* presents something of a problem. Regrettably I have been unable to examine any specimens and thus am unable to comment on myological features or to make any constructive observations except to consider the possibility of its relationship with the Cynodontini. The pattern of dentition, the number of branchiostegal rays (5 according to Gery, 1963), and the length of the pectoral fins may be shared specializations.

Gery (1963) considered, on the basis of cranial and scale morphology, that *Agoniates* is not related to the cynodontine fishes but is more closely related to the Bryconini.

DISCUSSION

The species comprising the tribe Cynodontini are seemingly adapted for a specialized predatory existence. Unfortunately, due to a complete lack of biological and ecological information, the exact nature of this mode of life is unknown.

Of course, other characoids have adopted the predatory roles but these have assumed the familiar 'pike-like' facies. Examples are to be found in the Hepsetidae, Ctenoluciidae and Acestrorynchinae. Unpublished myological studies of these taxa have shown that they can be clearly separated from other characoids on the basis of at least one shared skeleto-myological feature, namely the morphology of the *dilatator operculi* and its accommodating fossa. In all (apart from *Hepsetus*) the muscle originates from the ventral surface of the frontal and is directed through a tunnel, the roof of which is formed by the frontal and the floor by the autosphenotic, the bones being sutured along their lateral margins (noted in *Erythrinus* by Weitzman, 1964; in *Hoplias* by Alexander, 1964; in *Acestrorhynchus*, *Ctenolucius* and *Boulengerella* by Roberts, 1969).

Another characteristic of these pike-characoids is the relatively flat skull in which the long sphenotico-pterotic region provides an increase in the area of origin for the *adductor mandibulae* muscles. Also, as Alexander (1964) has pointed out in discussing *Hoplias*, these fish benefit from possessing long *dilatatores operculorum* muscles, since such muscles are probably used to boost the water currents entering the mouth, thereby assisting in the capture of prey.

The *dilatator operculi* is basically a parallel fibred muscle and in order for it to achieve the necessary force either it can operate over an increased distance to allow for the necessary shortening of the fibres, or it can increase the area of its origin and become pinnate, thus obtaining the same mechanical advantage.

Just which form the muscle takes will depend upon other demands imposed upon the cranium. Thus, in the pike-characoids, which present a 'streamlined' profile, the muscle is concealed below the cranial roof. Here, however, the area of origin is too restricted to allow for a well-developed pinnate form of the muscle, and reliance is placed on utilizing the orbital-opercular distance. In those characoids where the skull is vaulted the *dilatator operculi* can extend to the dorsal surface of the cranium to run obliquely downwards. Here the area of origin is greatly expanded, as in the Cynodontini, and the muscle is distinctly pinnate. It may be mentioned here that the characoid *Anodus* (Hemiodontidae; see Roberts, 1975) has a very large operculum. This fish is not a predator but seems to feed on plankton and, possibly, detrital material. Here, again, the *dilatator operculi* has become enormously developed and extends over the entire frontal region.

In the pike-characoids an increased area of origin for the *adductor mandibulae* is provided by the long sphenotico-pterotic border, with a consequent increase in the area of the hyomandibula. The advanced species of the Cynodontini have evolved a predatory facies not by elongation of the ethmoid or the postorbital skull region as in the pike-characoids, but by a reorientation of the jaw suspensorium. This is achieved by the quadrate and metapterygoid shifting into an almost perpendicular position, by correlated modifications to the hyomandibula (see remarks by Nelson, 1949: 505), by lengthening of the maxilla and the lower jaw, and by expansion of the dilatator fossa on to the dorsal surface of the cranium. It is interesting to note here the different reorganization involved in achieving the same 'solution' in the cyprinid *Macrochirichthys* (p. 245), where a reorientation of the muscles rather than of the bony supports seems to have occurred.

The lineage which gave rise to the Cynodontini would appear to have been an early off-shoot from the basal group which also gave rise to the Tetragonopterinae and related taxa. Somewhat parallel trends are seen in both the Cynodontini and Characini, producing specialists with elongate bodies, more scales, large mouths, raptorial dentition and a consequent parallel development of the cranial musculature. However, such an extreme form as *Rhaphiodon* has not arisen in the Characini.

The morphology of the cynodontine species suggests an existence at, or close to, the surface of the water, whereas the pike-characoids tend to occupy the mid-water levels. Thus, there is unlikely to be direct competition between these two groups.

ACKNOWLEDGEMENTS

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Finally, and not least, go my thanks to Dr R. H. Lowe-McConnell for providing information on living characoids and for sparing so much time in discussing them.

APPENDIX

Observations on the cranial anatomy of the cyprinid fish *Macrochirichthys macrochir* (Val.)

(Figs 22–24)

A remarkable example of parallelism is seen when the cynodontine characoid *Rhaphiodon vulpinus* is compared with the cyprinid *Macrochirichthys macrochir*, a species recorded from Thailand, Java, Sumatra, Borneo and Malaysia (Smith, 1945) and from China (Wu, 1964). (The term 'parallelism' rather than 'convergence' is used here because it is assumed that the cyprinoids and characoids share a common (albeit a relatively remote) ancestry, and thus have presumably inherited a common genetic capacity that will respond by producing similar adaptations to similar environmental pressures.)

Both *Rhaphiodon* and *Macrochirichthys* exhibit the same extreme elongation of body, inclination of the jaw, markedly elongate pectoral fins and position of median fins (cf. Figs 22 & 1C). However, the arrangement of the cranial muscles in *Macrochirichthys* differs quite considerably from those in *Rhaphiodon* (Figs 23 & 24).

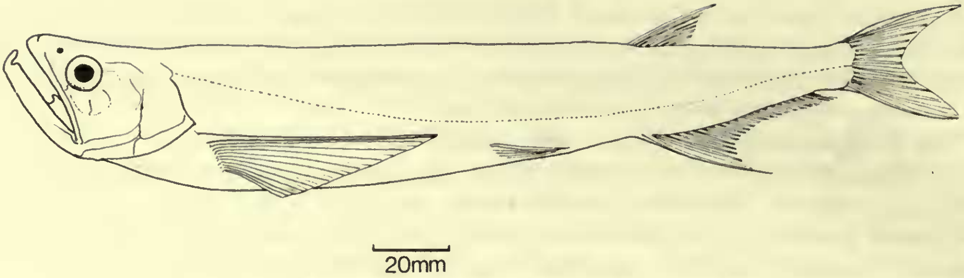

FIG. 22. *Macrochirichthys macrochir*, outline drawing.

The frontals provide attachment for epaxial musculature, which extends anteriorly as far as the ethmoid.

The *dilatator operculi*, which is such a prominent feature in *Rhaphiodon*, is reduced to a small element running from the sphenotic and pterotic to the edge of the operculum.

The *levator operculi* is large ; it originates along the entire pterotic border and runs along the medial surface of the operculum.

The *adductor operculi* joins the *levator* anteriorly (I am unable to determine the precise origin of the *adductor* from the single specimen at hand).

The facial muscles also show quite a departure from the arrangement in the characoid.

The external cheek muscle, the *adductor mandibulae* section A_1, originates from the quadrate and preoperculum and from the mass of the underlying section A_2. Insertion is along the lateral dorso-posterior border of the wide maxilla (both maxillary and premaxillary bones are firmly sutured for their entire lengths, thus together forming a thick, heavy upper jaw). This development of the insertion of A_1 suggests a more active role for the upper jaw than in *Rhaphiodon*.

Adductor mandibulae section A_2 originates from the hyomandibula to insert upon a wide aponeurosis. Medially there lies another element which also takes its origin from the hyomandibula. I cannot be certain whether this is A_2a or A_3 (following the nomenclature of Takahasi, 1925, this would be A_3). The muscle is greatly thickened antero-ventrally, its fibres being folded over and running almost perpendicularly to join those of the outer element.

The *levator arcus palatini* (Fig. 24) is a complex muscle originating both from the ventral surfaces of the frontals and from the sphenotic. An outer bundle of fibres is somewhat separated from the main element and inserts tendinously upon a small, anteriorly directed process of the hyomandibula. Posteriorly the main part of the muscle inserts in a hyomandibular fossa.

The *adductor arcus palatini* (AAP, Fig. 24) is a small muscle having a very narrow origin posteriorly on the parasphenoid ; it inserts ventrally on the metapterygoid. A thin fibrous sheet of connective tissue (TCT, Fig. 23) extends the length of the parasphenoid, and is closely applied to the metapterygoid laterally. The fibres within this sheet are orientated postero-ventrally at an angle of *c*. 30° to the horizontal.

The pectoral fin musculature closely resembles that of *Rhaphiodon*. The *abductor superficialis* is divided by a tendinous sheet that inserts along the proximal edges of the pectoral rays. The *arrector ventralis* runs from the cleithrum to insert via long tendons on to the first and second pectoral rays. I am unable to find the equivalent of the small 'depressor' muscle described in the Cynodontini (see p. 221).

The long dentary has the symphysial tip drawn out into a tooth-like process (see p. 244). The hyoid bars, urohyal and first basihyal are of similar shape to those elements in *Rhaphiodon*. The gill rakers of *Macrochirichthys* are reduced (as in *Rhaphiodon*); the pharyngeal teeth are in two rows and are thin and sharply pointed (an unusual feature among the cyprinids).

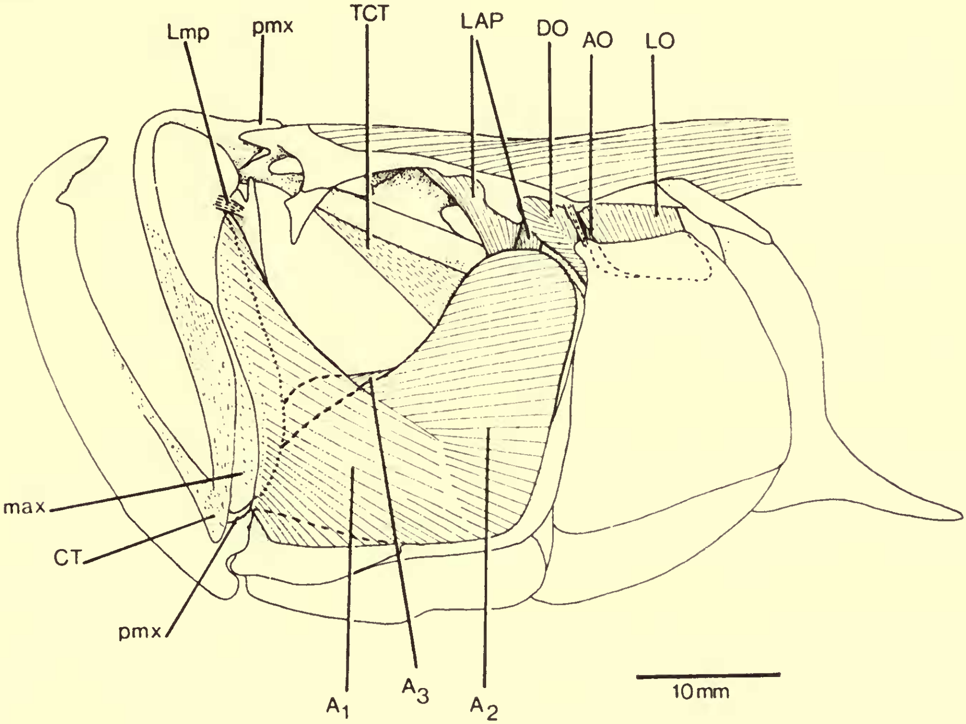

FIG. 23. *Macrochirichthys macrochir*, superficial facial musculature, lateral view. The dotted line indicates the border of the maxilla, the thick dashed lines, the borders of A_2 and A_3, and those on the operculum, the areas of the *levator* and *adductor operculi*.

The parasphenoid is straight and thickened; the orbito-sphenoid is sutured to the parasphenoid (features shown by *Rhaphiodon*).

One difference to be noted is that a ligament connects the pterotic to the operculum and not to the preoperculum, as in *Rhaphiodon*.

Another parallel feature shared with the characoid is the presence of many long intermuscular bones. However, these are not distributed throughout the *epaxialis* but are orientated cranio-caudally along the bases of the neural spines (the more

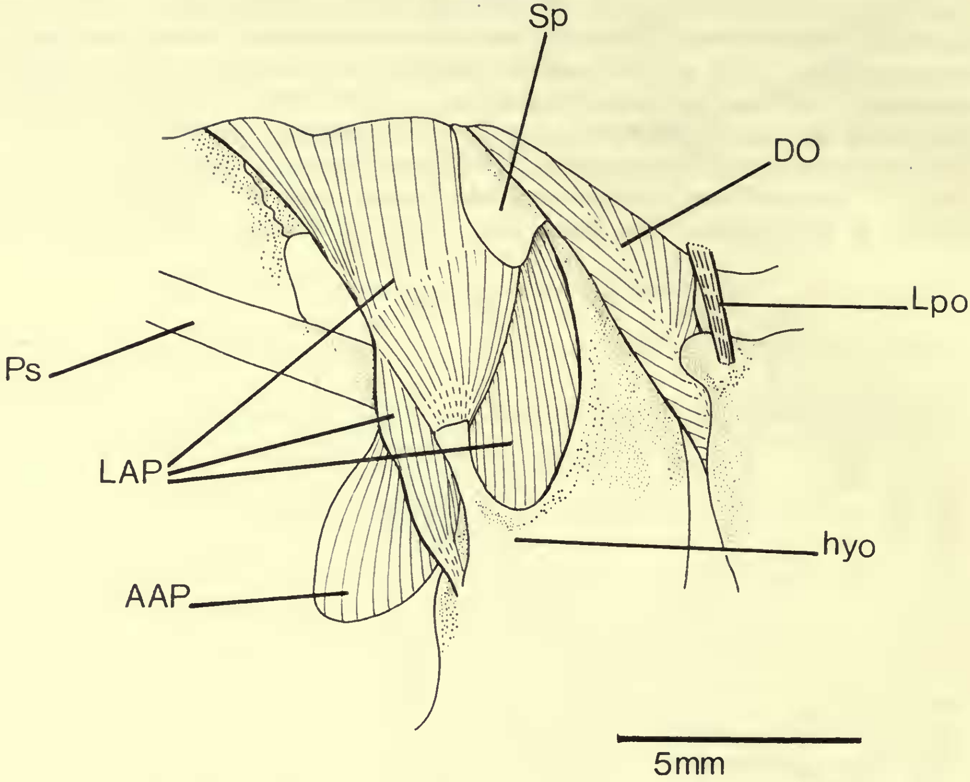

FIG. 24. *Macrochirichthys macrochir*, lateral view of the dorsal aspect of the hyomandibula showing the various insertions of the *levator arcus palatini*.

usual situation). Anteriorly they extend as bundles from the pterotic (as in *Rhaphiodon*).

One peculiar feature of *Macrochirichthys* is the development of the anterior supraneurals (predorsal bones). The first, second and third are thin, elongate structures, the first appearing almost to articulate with the long third neural spine (Fig. 25). This series of bones together forms a firm but flexible arc. This arrangement suggests a counteractant to stresses similar to those believed to occur in *Rhaphiodon* (p. 225) and again is indicative of some backward and upward movement of the skull when the fish is capturing its prey.

The single large symphysial 'tooth' of *Macrochirichthys* possibly performs a more manipulative function than do the slender teeth of *Rhaphiodon* (p. 225). Behind this symphysial projection the dentary is indented, indicating that the prey may be held transversely. A similar strong tooth-like process and jaw indentation can be found in other cyprinoids, e.g. *Opsariichthys uncirostris*, *Barilius bola* and some *Paralaubuca* species.

No stomach contents were present in any of the three specimens of *Macrochirichthys* examined.

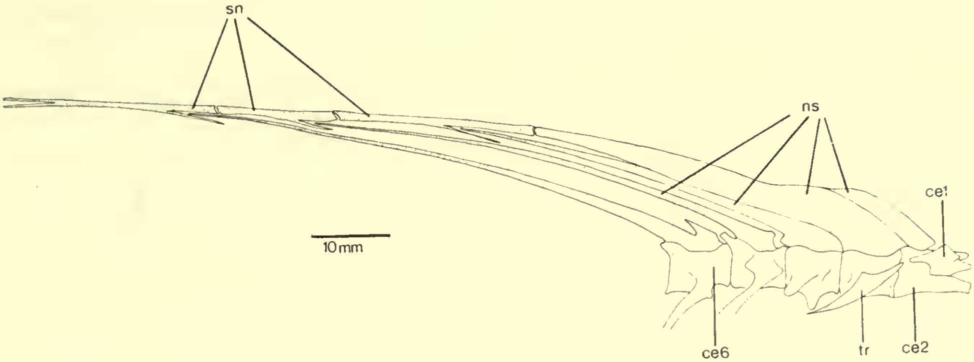

FIG. 25. *Macrochirichthys macrochir*, lateral view (right) of the anterior part of the vertebral column.

The facial musculature of *Macrochirichthys* closely resembles that of *Opsariichthys* (see Takahasi, 1925; Winterbottom, 1974). Furthermore, a quadrate-metapterygoid fenestra is present. This feature was considered by Greenwood *et al.* (1966) to be a primitive character for the cyprinoids. However, Gosline (1973) has pointed out that the fenestra has a functional significance in providing increased area for the *adductor mandibulae*, that it has probably evolved several times over, and that it is the form of the architecture of the suspensorium in which the fenestra has developed that is the indicator of relationship.

The fenestra in *Macrochirichthys* is small compared with that in *Rhaphiodon* and the actual size of the opening appears to have little to do with the degree of development of the *adductor mandibulae* (as observed in other characoids). The presence of the fenestra undoubtedly confers a greater mobility on the suspensorial elements, enabling them to reorientate more readily to the stresses induced by a highly developed (and developing) muscle system.

Macrochirichthys is a highly specialized cyprinid which may have evolved from the same ancestral lineage as did *Opsariichthys*. It is hoped to test this speculation when further material is available.

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